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PLANT-HERBIVORE INTERACTIONS ON THE YUKON-KUSKOKWIM DELTA: THE EFFECT OF GOOSE HERBIVORY ON ARROWGRASS

A

THESIS

Presented to the Faculty

of the University of Alaska Fairbanks

in Partial Fulfillment of the Requirements

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DOCTOR OF PHILOSOPHY

By

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Fairbanks, Alaska

December 1996

PLANT-HERBIVORE INTERACTIONS ON THE YUKON-KUSKOKWIM DELTA:

THE EFFECT OF GOOSE HERBIVORY ON ARROWGRASS

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ABSTRACT

I examined effects of herbivory by black brant geese (*Branta bernicla nigricans*) on the small herbaceous perennial *Triglochin palustris* (arrowgrass) in a subarctic saltmarsh in SW Alaska. I investigated effects of biomass removal, and indirect effects of geese (changes in resource availability and competition) to compare the role of selective herbivory in this mixed-species environment with that of herbivory in monospecific saltmarsh communities.

I manipulated nutrient availability, light availability, and salinity in a transplant experiment, and manipulated size of arrowgrass, and neighbor size and feces deposition in exclosure experiments. Additional experiments examined relationships between size, biomass allocation, survival and reproduction, and explanations for low rates of sexual reproduction in arrowgrass. A cellular automata model was used to investigate potential long-term effects of changes in grazing intensity.

Direct effects of geese were smaller than indirect effects: biomass removal had little effect on rates of population growth or plant size, and resulting changes in biomass allocation did not affect survival or reproduction. For unclipped arrowgrass, feces deposition resulted in increased competition for light, which was ameliorated by consumption of neighboring plants, but some species may provide protection from grazing. Expansion into neighboring communities is limited by physical factors on the sea-side end of the distribution, and by competition for light and high selectivity on the inland end. Overall effects of changes in grazing pressure will depend on changes in goose foraging behavior and selectivity.

Trade-offs exist between sexual reproduction and all other functions, and sexual reproduction may increase risk of herbivory. Goose effects occur at several spatial and temporal scales: immediately (through biomass removal), within a growing season (through changes in competition and resource availability), over several growing seasons (through feedbacks to foraging behavior), and over long periods (through changes in reproduction). Model results suggest increased grazing intensity may not decrease arrowgrass populations under some conditions, and that spatial distribution of geese affects population dynamics of arrowgrass.

There is no evidence that feces deposition results in greater productivity of preferred species. More detailed knowledge of goose foraging behavior at several spatial and temporal scales is needed in order to understand the dynamics of this system.

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CHAPTER ONE: INTRODUCTION

LITERATURE REVIEW

Emphases in herbivory research

Between the mid 1980's and mid 1990's, research on herbivory experienced a distinct shift in emphasis. In the mid to late eighties, a hotly debated point concerned the existence of 'overcompensation': whether herbivory can have an overall positive effect on the plants being eaten (e.g. Choudhury, 1984; Belsky, 1986; McNaughton, 1986; Verkaar, 1986; Crawley, 1987; Paige and Whitham, 1987), and whether this constitutes a mutualism between plants and their herbivores (e.g. Owen, 1980, 1982; Owen and Wiegert, 1981; Thompson and Uttley, 1982; Coughenour, 1985; Lam and Dudgeon, 1985; Aarssen and Turkington, 1987; Hendrix and Trapp, 1989; Westoby, 1989). Much of the disagreement in this debate stemmed from confusion over what exactly constituted 'herbivore effects' (Belsky, 1986; Crawley, 1987; Brown and Allen, 1989; Westoby, 1989; Pollard, 1992): some workers included only direct effects of herbivory (i.e. biomass removal; e.g. Inouye, 1982; Hendrix and Trapp, 1989) while others included indirect effects of herbivory presence such as fertilization through deposition of feces (e.g. Stenseth, 1978; McNaughton, 1979; Bazeley and Jefferies, 1985, 1986; Cargill and Jefferies 1984a,b), urine (Woodmansee, 1978; Schimel et al., 1986) or honeydew (Owen and Wiegert, 1981), or changes in community composition as a result of selective herbivory (McNaughton, 1979; Pastor et al., 1988). As studies accumulated it became apparent that whether herbivores benefitted plants depended on whether affected plants were being compared with ungrazed individuals of the same species in the absence of herbivores, ungrazed individuals in the presence of herbivores, or to individuals of other species, as well as on the particular conditions under which herbivory occurred

and the time scale on which its effects were measured (Brown and Allen, 1989). By the late 1980's research emphasis had shifted to elucidating the conditions under which various responses might be expected, and the mechanisms underlying positive responses (e.g. Maschinski and Whitham, 1989; Georgiadis et al., 1989; Hik and Jefferies, 1990; Aarssen and Irwin, 1991; Doak, 1991; Oesterheld and McNaughton, 1991; Reichman and Smith, 1991). Herbivory often is selective at the species level (e.g. Crawley, 1983, 1987; Archer and Detling, 1984; Kinsman and Platt, 1984; Ingham and Detling, 1986; Pastor and Naiman, 1992; Brown and Stuth, 1993), and it was pointed out several decades ago that the main effect of herbivory may often be to change competitive interactions between two individuals or two species (Sibma et al., 1964, in Rauscher and Feeney, 1980; Harper, 1977; McNaughton, 1978). Although relationships between herbivory, abiotic factors, and interspecific interactions have been well studied in intertidal and marine systems (e.g. Lubchenco and Gaines, 1981; Paine and Levin, 1981; Duggins and Dethier, 1985; Moreno and Sutherland, 1982), in terrestrial systems the importance of herbivory for changes in competition is often implied (e.g. Crawley, 1983; Ellison, 1987; Hik et al., 1992) but seldom explicitly examined in natural systems (Louda et al, 1990, but see Fowler and Rauscher, 1985; Bergelson, 1990). In this thesis, I address the relationships between direct effects of herbivory (biomass removal), effects of herbivory on the plant environment, and the effects of herbivory on competition, using goose herbivory on a small perennial herbaceous plant in a subarctic saltmarsh as my model system.

Ecology of saltmarsh plants

Until recently, most studies of individual saltmarsh species have focused on one of two general areas: physiological responses of plants to abiotic stressors (particularly salinity and

waterlogging; e.g. Jefferies et al., 1979; Mendelssohn and Seneca, 1980; Cooper, 1982; Jefferies and Rudmik, 1991; Srivastava and Jefferies, 1995) and the distribution of species relative to abiotic factors such as salinity, nutrient availability, soil redox potential, and flooding (e.g. Howes et al., 1981; Hutchinson, 1982; Vince and Snow, 1984; Earle and Kershaw, 1989; Kincheloe and Stehn, 1991; Bertness et al., 1992a,b). In contrast, research on the effects of goose herbivory on plants in subarctic saltmarshes has concentrated primarily on effects at the community and ecosystem level, such as effects on net above-ground primary productivity (Cargill and Jefferies, 1984b; Groenendijk, 1984; Groenendijk and Vink-Lievaart, 1987; Hik and Jefferies 1990; Bélanger and Bédard, 1994; Gauthier et al., 1995), nitrogen availability and cycling (Cargill and Jefferies 1984b; Bazely and Jefferies 1985, 1989; Ruess et al., 1989) and species composition and successional rates (Bazely and Jefferies 1986; Hik et al. 1992; Bélanger and Bédard, 1994). Much of this work was performed by Jefferies and his co-workers at La Pérouse Bay, a subarctic saltmarsh on the coast of Hudson Bay, Manitoba, Canada. They demonstrated that in monospecific stands of preferred species of forage such as *Carex subspathacea* and *Puccinellia phryganodes*, moderate levels of herbivory by lesser snow geese (*Anser caerulescens caerulescens*) can result in increased above-ground productivity through increased rates of nitrogen cycling (Bazely and Jefferies, 1986, 1989; Cargill and Jefferies, 1984a) , whiereas heavy trampling by geese can increase soil salinity (Srivastava and Jefferies, 1996). Nonetheless, geese often graze in mixed-species stands, and these herbivores can be highly selective foragers (Prevett et al., 1985; Prins and Ydenberg 1985; Sedinger and Raveling, 1986; Thomas and Prevett, 1986). In these habitats, only some species are consumed but all species are exposed to effects of geese such as fertilization and trampling. If species differ in their ability to tolerate or respond to the indirect effects of geese, then the community-level response to the presence of geese in mixed species

stands may differ from that in monospecific stands. In this study I test whether the conclusions from the La Pérouse Bay saltmarsh are applicable to mixed-species habitat in an Alaskan saltmarsh.

In the past five years, studies of saltmarsh plant ecology have started to integrate abiotic and biotic factors. The potential for plants species to act as facilitators for other species through modification of the physical environment has been demonstrated by Bertness and his co-workers in a New England saltmarsh (Bertness, 1991; Bertness and Shumway, 1993; Bertness and Hacker,1994), and by Castellanos et al. (1994) in a Spanish saltmarsh . The view of the role of herbivores in these systems also is changing. For example, Ellison (1987) reported that the distribution and abundance of *Salicornia europaea* was determined by interactions between disturbance (deposition of wrack), seed dispersal, interspecific competition, and herbivory. Hik et al. (1992) showed that geese can delay changes in species composition in a subarctic saltmarsh, whereas in the same system Srivastava and Jefferies (1996) demonstrated that grubbing by geese can lead to higher evaporation rates and thus contribute to desertification. As a group, these studies reveal that although abiotic factors play a large role in structuring of the saltmarsh community, other plant species and herbivores (and probably other taxonomic groups) can modify the physical environment, resulting in complex and site-specific interactions between biotic and abiotic interactions. This study examines the potential for such interactions in a relatively species-rich habitat in a subarctic saltmarsh.

Interaction modifications and herbivore selectivity

Most research in ecology involves studies on at most two species at a time (Kareiva, 1994). If more complex systems (i.e. all real life systems) involves the modification of the

relationship of two species by a third species, then we cannot predict the behavior of such systems based on knowledge of pair-wise interactions (Billick and Case, 1994; Wootton, 1994; Adler and Morris, 1994). To most biologists the existence of such interactions is obvious; the more interesting question is whether they can be ignored without losing the ability to predict population dynamics (Adler and Morris, 1994). One situation in which interaction modifications clearly exist is a system in which an herbivore is selective: provided each plant species is palatable to the herbivore, the outcome of trials including several plants and the herbivore cannot be predicted from knowledge of all pairwise interactions (Brown and Stuth, 1993). A second potential interaction may result from the existence of 'associational refuges': the presence of some species may decrease the probability that an herbivore can locate individuals of a forage species (McNaughton, 1978; Atsatt and O'Dowd,1976; Hay, 1986; Ellison, 1987). Again, although it seems obvious that such interactions exist, few studies have demonstrated that they are important for plants at the population level.

Scaling up from individuals to populations

Populations often are treated as aggregations of identical individuals (DeAngelis and Gross, 1992). This violates two inherent properties of nature: (1) individuals within a population vary, and (2) individuals, particularly in sessile species, interact more with nearby individuals than with ones that are farther away (DeAngelis and Gross, 1992; Tilman, 1994). Both of these principles have implications for the ability to detect the mechanisms by which ones species might affect interactions between other species. For example, imagine a three-species system: two plant species (A and B), and an herbivore. In the absence of herbivores, A and B compete equally. Assume that herbivory alters the competitive ability of plant species A (e.g. through a change in

root to shoot ratio) but that this is not reflected in population dynamics of that species in monoculture. In the presence of the herbivore, the competitive relationship between A and B is altered and population dynamics can no longer be predicted from knowledge of all pairwise interactions. Understanding this three-species interaction requires an understanding of effects of the herbivore on species A at the individual level. Similarly, if interaction modifications depend on the close physical location of all three species simultaneously, the spatial distribution of individuals may affect population dynamics.

Acknowledging the existence of spatial heterogeneity in populations, not just in terms of population size but also in terms qualities of individual plant (i.e. size, nutritional content, etc.), also leads to the potential for feedbacks from plant populations following herbivory to herbivore behavior and foraging efficiency. Feedbacks from plants to herbivores have received much interest in the literature on plant defence (e.g. in the form of induced defences; Karban and Myers, 1989), and optimal foraging theory predicts changes in behaviour of individuals with changes in the quality of food items (Pyke et al., 1977). A few studies have linked effects of herbivores on individual plants to herbivore populations through effects on nutrient flow (e.g. Pastor and Naiman, 1992; Pastor et al., 1988; Holland et al., 1992), but the effects of local changes in plant characteristics and species composition on future use of that area by noninsect herbivores are not well understood for most systems (but see Ward and Saltz, 1994). In this study I present results of a small experiment that examines changes in probability of herbivory with changes in size of the forage species and species composition. Although my experiment is short-term and small-scale, it has implications for longer-term feedbacks from plant communities to herbivores in saltmarsh systems.

There has been a great increase recently in interest in 'individual-based models' to overcome the problems inherent in treating all individuals in a population as equal (DeAngelis and Gross, 1992). Some ecologists have split individuals into several groups based on characteristics assumed be important at the population level (e.g. age- or stage-transition population models), whereas others follow individuals as discrete entities (e.g. cellular automata models; DeAngelis and Rose, 1992). In the final chapter of this thesis, I attempt to synthesize information from the experimental chapters by using the latter approach and present results from a individual-based, spatially explicit model that allows me to examine some potential consequences of the individual-level effects for the population level.

APPROACH AND SYSTEM DESCRIPTION

This study examined the effect of goose herbivory on a small herbaceous perennial in a subarctic saltmarsh. Rather than focusing on one hierarchical level and examining many species simultaneously, I concentrated on one plant species but performed measurements over a range of hierarchical scales: on plant parts (e.g. nitrogen concentration); individual plants (size and biomass allocation); the population level (density and distribution); the community level (species composition); and the ecosystem level (e.g. aboveground biomass, above-ground total nitrogen, rates of nitrogen mineralization in soil). I performed experiments with three general goals in mind: 1) to explicitly distinguish between direct effects of herbivores (biomass removal), indirect effects mediated through changes in the abiotic environment, and indirect effects mediated by changes in the competitive environment; 2) to link physiological and morphological effects of herbivores on

individuals of the forage species with effects at the population and community levels; and 3) to examine feedbacks from the plant community to herbivore foraging effectiveness.

I used a subarctic saltmarsh on the coast on the Yukon-Kuskokwim (Y-K) Delta in south-western Alaska as my model system. Populations of nesting Pacific black brant (*Branta bernicla nigricans*), cackling Canada geese (*B. c. minima*), white-fronted geese (*Anser albifrons*) and emperor geese (*A. canagicus*) are extremely high in this area. Some aspects of these populations such as population dynamics, nutritional requirements, and behavior, have been well studied, particularly for cackling Canada geese (e.g. Sedinger, 1984, 1986, Sedinger and Raveling, 1984, 1988, 1990;) and black brant (Sedinger and Flint, 1991; Anthony et al., 1995; Flint et al., 1995; Sedinger et al., 1995*a*,*b*), and to a lesser extent for emperor geese (Eisenhauer and Kirkpatrick, 1977; Shmutz, 1993) and white-fronted geese (Budeau et al., 1991). In contrast, current knowledge of the vegetation is limited to descriptions of species (Hultén, 1962) and their distributions relative to edaphic characteristics (Kincheloe and Stehn, 1991) or wildlife habitat (Burns, 1964; Holmes and Black, 1973; Eisenhauer and Kirkpatrick, 1977; Babcock and Ely, 1994).

The landscape in the study area is dominated by a myriad of tidal rivers, small sloughs, and countless ponds. Geese forage in two distinct types of habitat: the *Puccinellia phryganodes* - *Carex subspathacea* 'grazing lawns' located on mudflats along the coast and on the edges of small ponds, and, later in the season, in the mixed species communities on slough levees (Sedinger and Flint, 1995; *personal observation*), which are more species rich than the grazing lawns (Kincheloe and Stehn, 1991). Rates of food intake of brant geese and cackling Canada geese are probably limited by passage rates through the gut (Buschbaum et al., 1986; Sedinger and Raveling, 1988), resulting in strong selection for plants with a low fiber and high-protein content (Sedinger and

Raveling, 1984; Gauthier and Bédard, 1990). Herbivory in this habitat is highly selective: species such as *Triglochin palustris*, *Deschampsia caespitosa*, *Potentilla egedii* and *Carex ramenskii* are important components of the diet while other species (e.g. *Salix* and *Elymus arenarius*) are not consumed (Sedinger, 1984; *personal observation*). The effect of herbivory on competition between plants should be greatest when the environment severely limits the opportunities for compensatory regrowth (Louda et al., 1990); this is probably an apt description of subarctic saltmarshes, where plants face short growing seasons, low availability of nitrogen (Cargill and Jefferies, 1984a), variable soil salinity, and waterlogged soils (Adam, 1990). The combination of selective grazing and levels of abiotic stress led me to expect interactions between direct effects of geese on plants, and indirect effects through changes in nutrient availability and competition in the slough levee community.

My study species was *Triglochin palustris* L. (arrowgrass: Juncaginaceae). This plant has a high protein content, and is highly preferred by geese of several species (Sedinger and Raveling, 1984; *personal observation*). It is of particular importance to goslings, providing between 44 and 98% of the diet of cackling Canada goslings prior to fledging (Sedinger, 1984; Sedinger and Raveling, 1984). The small size of arrowgrass makes it possible to measure whole plants, including roots; this is particularly important given our extremely poor understanding of the effect of herbivory on root systems (Marquis, 1992). Transplanting arrowgrass early in the growth season does not appear to affect survival (Chapter 2). Arrowgrass reproduces primarily vegetatively through the production of bulbs (personal observation) and is referred to variously as being stoloniferous (Hultén, 1968) or rhizomatous (Welsh, 1974); I have observed 'stolons' both above and below ground, but for sake of consistency will refer to it as stoloniferous. Due to its size and mode of reproduction (stolons are usually only a few centimeters long, *personal*

observation), interspecific interactions are likely to occur on a very small scale. In addition to the importance of this plant to geese and the ease with which it can be manipulated, I selected this species because most work on herbivory has been done on grasses, woody perennials, and short-lived monocarpic species, while herbaceous perennials have received little attention (Doak, 1991; Mulder and Harmsen, 1995). The growth form of arrowgrass differs from that of sedges and grasses in this habitat, most notably in its smaller size and much smaller proportion of biomass below ground (*personal observation*), and it is therefore likely to respond differently to biomass removal.

Studies of arrowgrass have been limited to general descriptions (Looman, 1976), investigations of its cyanogenic properties (Eyjólfsson, 1970) and nutritional qualities (Sedinger, 1984; Thomas and Prevett, 1986), although physiological changes in response to salinity have been examined in a sister species, *Triglochin maritima* (Jefferies and Rudmik, 1991). One goal of this thesis was to provide some basic ecological and life-history information for this species.

OUTLINE OF THE THESIS

My thesis contains three chapters that outline experimental work. In Chapter 2, I describe a series of transplant experiments used to examine the roles of light availability, nutrient availability, salinity, and their interaction in affecting arrowgrass size and distribution. Results focus primarily on the level of individual plants. This study generated several hypotheses regarding direct and indirect effects of goose herbivory on arrowgrass. In Chapter 3, I test these hypotheses using a combination of manipulative experiments and simple herbivore-exclusion experiments. In addition, I investigate the potential for other species to provide refuges from herbivory.

Chapter 4 focuses on two aspects of the basic biology of this species: the relationship between size and biomass allocation, and subsequent survival and reproduction, and potential causes of the low and highly variable rates of sexual reproduction. This information provides a link between effects of geese on arrowgrass individuals (changes in size and biomass allocation) and potential population level effects. Chapter 5 consists of two parts: a general discussion of experimental results; and an attempt to synthesize these results in the form of a simple qualitative model that incorporates information from the experimental chapters. This generated new hypotheses regarding longer-term dynamics of arrowgrass, and provided insights into areas where current knowledge is insufficient and future research should be concentrated.

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CHAPTER TWO:

EFFECTS OF ENVIRONMENTAL MANIPULATIONS ON *TRIGLOCHIN PALUSTRIS*: IMPLICATIONS FOR THE ROLE OF GOOSE HERBIVORY IN CONTROLLING ITS DISTRIBUTION[1]

SUMMARY

(1) Arrowgrass (*Triglochin palustris*) is a preferred forage species of geese in the Yukon-Kuskokwim Delta (SW Alaska) where it is found primarily on slough levees in coastal areas. Geese may affect nutrient availability, interspecific light competition, and salinity. These variables were manipulated in order to identify interactive effects of interspecific competition and abiotic factors on arrowgrass size, biomass allocation and distribution, which are likely to be significant in relation to the effects of herbivory on arrowgrass abundance and distribution.

(2) Arrowgrass individuals were transplanted from two slough levee communities to the same two communities and to the adjacent slough margin and wet *Carex* meadow communities. Geese were excluded and nutrient availability, light competition and salinity levels were manipulated.

(3) Under control light levels, fertilization had a negative effect on plant biomass and allocation to bulbs. Under fertilization and decreased competition for light, plant biomass was not significantly different from that of control plants. Fertilization appears to have a negative effect on arrowgrass as a result of increased competition for light.

(4) Plants in the slough margin habitat were smallest, had the lowest allocation to leaves and stolons, and the lowest N concentrations and total N mass. Results from the fertilization treatment suggest plants in this community are limited primarily by physical factors.

(5) Plants in the *Carex* wet meadow had higher allocation to leaves than in other communities under unfertilized conditions, but decreased allocation to leaves under fertilization. Plants in this community appear light- and nutrient-limited under unfertilized conditions, and primarily light-limited under fertilization.

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(6) Three hypotheses regarding the role of goose presence in controlling arrowgrass distribution emerge: 1) feces deposition has a negative effect on arrowgrass, 2) this negative effect is ameliorated by consumption of neighbours, and 3) the combination of high light competition and highly selective foraging for arrowgrass limit expansion of arrowgrass into the *Carex* meadow community.

Key-words: goose herbivory, subarctic salt marsh, biomass allocation.

INTRODUCTION

The presence of geese in subarctic salt marshes can have large effects on salt-marsh ecosystem function (e.g. Bazely & Jefferies 1986, 1989; Cargill & Jefferies 1984b; Ruess, Hik & Jefferies 1989; Kerbes, Kotanen & Jefferies 1990). Most work on effects of goose herbivory on vegetation has focused on ecosystem- and community-level processes, such as net above-ground primary productivity (NAPP; Cargill & Jefferies 1984b; Hik & Jefferies 1990), nitrogen availability and cycling (Cargill & Jefferies 1984b; Bazely & Jefferies 1985, 1989; Ruess et al. 1989), and species composition and successional rates (Bazely & Jefferies 1986; Hik, Jefferies & Sinclair 1992). However, in many communities geese are highly selective foragers (Thomas & Prevett 1980; Sedinger & Raveling 1986; Prevett, Marshall & Thomas 1985; Prins & Ydenberg 1985), and preferred forage species are not always dominant. Goose herbivory then has the potential to affect forage species not only through biomass removal and fertilization of that species, but also indirectly, through shifts in competitive interactions among plant species and between grazed and ungrazed conspecifics both as a result of differential biomass removal and in response to changes in resource availability.

Studies of salt-marsh plant species have tended to concentrate on physiological properties, such as tolerance of plants to salinity and waterlogging (e.g. Jefferies, Rudmik & Dillon 1979; Mendelssohn & Seneca 1980; Cooper 1982; Jefferies & Rudmik 1991), or on describing species distributions relative to edaphic factors such as salinity, soil-redox potential, flooding, and nutrient

availability (e.g. Howes, Howarth, Teal & Valiela 1981; Hutchinson 1982; Vince & Snow 1984; Kincheloe & Stehn 1991; Bertness, Gough & Shumway 1992; Bertness, Wikler & Chatkupt 1992). Recently, attention has focused on the relative importance of abiotic factors versus biotic interactions, and results from a number of studies suggest that competition and facilitation play a major role in the structuring of salt-marsh communities (Snow & Vince 1984; Bertness & Ellison 1987; Ellison, 1987; Bertness 1991; Pennings & Callaway 1992; Bertness & Shumway 1993; Bertness & Hacker 1994; Castellanos, Figueroa & Davy 1994). The role of herbivores in this process has been alluded to (Bazely & Jefferies 1986; Ellison 1987; Iacobelli & Jefferies 1991; Hik et al. 1992), but it is not understood how the interactions of herbivores, other plant species, and abiotic factors affect the establishment and growth of individual salt-marsh plants. This study was designed to identify the potential for the presence of such interactions as they affect one focal species.

The Yukon-Kuskokwim Delta contains high concentrations of nesting black brant (*Branta bernicla nigricans* Lawrence), cackling Canada geese (*B. canadensis minima* Ridgway), whitefronted geese (*Anser albifrons* Scopoli) and emperor geese (*A. canagicus* Sevastianov). Food intake of brant and cackling Canada geese is often limited by throughput rate (Sedinger & Raveling 1988), and both are highly selective foragers. Although goose foraging ecology and nutritional requirements have been studied (e.g. Sedinger 1984; Sedinger & Raveling 1984, 1986, 1988), knowledge of the vegetation is limited primarily to descriptions of species distributions relative to edaphic characteristics (Kincheloe & Stehn 1991). Our study species, *Triglochin palustris* L. (arrowgrass; Juncaginaceae) is a preferred forage species for cackling Canada geese (Sedinger & Raveling 1984) and for brant geese (pers. obs.) and has a high protein content and low fibre content (Sedinger & Raveling 1984; Thomas & Prevett 1986). Arrowgrass is of particular importance to goslings, which probably have protein-limited growth rates: 44-98% of the diet of

cackling Canada gosling diet before fledging may consist of arrowgrass (Sedinger 1984; Sedinger & Raveling 1984).

The objective of this study was to examine experimentally the interactive effects of interspecific plant competition, and abiotic factors on the growth of arrowgrass, which mimick the effects of herbivory by geese on plants of this species. We tested the following sets of hypotheses:

1. Additions of nutrients and fresh water to plants, and a decrease in competition for light, will change arrowgrass size and biomass allocation. Specifically, the addition of nutrients and fresh water will increase plant size and allocation to leaves, while reduced light competition will increase plant size but decrease allocation to leaves. The effects of nutrient addition, fresh water addition, and decrease in light competition will be additive. The expectations for changes in allocation pattern come from the concept of adaptive root to shoot ratio, where plants should maximise the effort spent on procuring limiting resources, and minimise effort spent on procuring non-limiting resources (e.g. Chapin 1980; Givnish 1983; Bloom, Chapin & Mooney, 1985; Tilman 1988).

2. Nutrient availability, light availability, and salinity determine the distribution of arrowgrass. Low nutrient availability and high salinity prevent arrowgrass from extending its distribution towards sloughs at the study site, while low light availability prevents arrowgrass from extending its distribution further inland.

3. Ecotypic differences and the environment experienced previously by individuals determine the magnitude of the response to manipulations of nutrients, salinity and light.

We used nutrient availability, light availability, and soil salinity as our experimental variables because they are likely to be affected by the presence of geese. Arctic and sub-arctic systems frequently have low nitrogen availability due to low decomposition and mineralization rates during the short, cold growth season (Cargill & Jefferies 1984a; Nadelhoffer et al. 1991;

Kielland & Chapin 1992); feces deposition can increase nitrogen availability by increasing nitrogen cycling rates (Cargill & Jefferies 1984b; Ruess et al. 1989). Trampling and consumption of neighbours can increase light availability and create microsites of disturbance. Geese may increase soil salinity through soil compaction and increased evaporation following reduction in plant cover (Iacobelli & Jefferies 1991; Bertness, Gough & Shumway 1992; Bertness & Hacker 1994; Callaway 1994), and greenhouse studies suggest that the growth of arrowgrass is reduced by soil salinities greater than 10g of dissolved solids per litre (C. Mulder, unpublished data).

Zonation is a common phenomenon in all salt marshes, and there is evidence that species distributions are often limited by physical stress on the low-resource (usually seaward) end of the distribution, and by competitive interactions on the high-resource end (Snow & Vince 1984; Bertness 1991, 1992; Pennings & Callaway 1992; Bertness & Hacker 1994). Understanding the importance of nutrients, light and salinity in affecting arrowgrass distribution provides a basis for determining the role of herbivores in positioning and maintaining these boundaries.

METHODS

Study system

The study was conducted at the Tutakoke River Black Brant study site during June and July of 1992. This site encompasses approximately 8 km^2 and is located on both sides of the Tutakoke River, 0.5 km inland from the Bering Sea coast on the Yukon-Kuskokwim Delta (southwestern Alaska; 61°15'N, 165°30'W). The vegetation is described in detail in Kincheloe and Stehn (1991).

Arrowgrass grows along slough levees and along the edges of small mud ponds (Fig. 1). It is a small (in this habitat usually 3-15 cm high, <40 mg dry weight) stoloniferous perennial that produces bulbs during the growth season. Our observations suggest that these bulbs very seldom emerge until the following spring, when the connecting stolon has completely decomposed. Sexual

reproduction is rare in this habitat (pers. obs.). Because identification of vegetative offspring following overwintering is virtually impossible, this study was limited to one growth season. Emergence of arrowgrass in 1992 was first noted on 14 June, approximately 2 weeks later than during the three years following (pers. obs.).

Brant and cackling Canada geese move onto slough levees during the later stages of brood rearing. They consume only aboveground portions of arrowgrass, although the much less numerous emperor and whitefronted geese may also grub for bulbs prior to snow melt (Budeau, Ratti & Ely 1992).

The study used transplanted individuals because arrowgrass is rare or absent in two of the four communities studied, and because the effects of community origin of the plants were of interest. Arrowgrass is highly tolerant of transplanting and its small size facilitates excavation. The small size of arrowgrass compared to most neighboring species (where it is abundant it comprises only approximately 4% of aboveground biomass) also simplifies the interpretation of interspecific interactions: arrowgrass is unlikely to cause significant depletion of resources available to competitors. Competitors can therefore affect resources available to arrowgrass, but the effect of arrowgrass on competitor growth is probably insignificant, and unlikely to result in a change in competitive ability of neighbours (Goldberg, 1990).

Experimental Design

The experiment used plants transplanted into a split-split plot design, with transects as blocks, four community types at the whole plot level, four or seven treatments at the subplot level, and two transplant origins at the sub-subplot level (see Fig. 2 for the lay-out within a transect, and descriptions below). This was replicated ten times (ten transects) over a distance of 1km for a total of 1760 plants.

Transects

On 15-17 June, 1992, ten transects approximately 15m in length were laid out perpendicular to two small (1-2m wide) sloughs (five on each slough). Transects were located over approximately 1 km, and were selected based on presence and similarity of the plant communities located along them, absence of parallel sloughs or other obvious hydrological features, and a minimum distance of 10m to the nearest transect. Slough water salinity ranged from $19^{0}/_{00}$ to $26^{0}/_{00}$ (mean = $21.3^{0}/_{00}$, early June to early August 1993 data, B. Person, unpublished data), while surface soil salinity in early June ranged from $2.7\ ^{0}/_{00}$ to $18.7\ ^{0}/_{00}$ (C. Mulder, unpublished data).

Communities

Four communities were defined along each transect (Fig. 1). Community 1 was at the slough margin inside the channel (mean distance to mean high water line [MHWL] = -0.7m), was flooded during high tide twice daily, and consisted of an almost monotypic stand of *Carex ramenskii*. Community 2 was located on the slough levee (mean distance to MHWL = +0.9m) and consisted of a mixture of monocotyledons and dicotyledons, including *Elymus arenarius* L., *Chrysanthemum arcticum* L., *Ligusticum scoticum* L., *Deschampsia caespitosa* (L.) Beauv., *Puccinellia phryganodes* (Trin.) Scribn. & Merr., *Potentilla egedii* Wormsk., *Carex ramenskii* Kom., *Carex glareosa* Wahlenb., and *Salix ovalifolia* Trautv. Community 3 was located further from the slough channel ("lower slough levee"; mean distance to MHWL = 6.7m) and had vegetation similar to that of community 2 but with greater monocotyledon abundance. Community 4 was located at the edge of a "*Carex* wet meadow" (mean distance to MHWL = 14.5m); *Carex ramenskii* and *C. glareosa* were dominant in this community. Communities 2, 3, and 4 were typically flooded only at extreme high tides and during spring and fall storms. Arrowgrass is found predominantly in communities 2 and 3 ("slough levee habitat") only.

Treatments and Origins

Along each transect four treatment plots (0.5m*0.5m) were established 0.5 m apart in communities 1 and 2 (Fig. 2). Treatments consisted of a 2*2 factorial design, with two levels of fertilization (not fertilized or fertilized) and two levels of water addition (fresh water or slough water). In communities 3 and 4 three additional treatments were included: (1) reduced competition for light ("light") (2) fertilization + light, and (3) fertilizer+fresh water+light (Fig. 2). Light treatments were not applied in communities 1 and 2 because percent cover in these communities was low and competition for light was already minimal. Within each community, plots were arranged parallel to the slough bank, and order of treatment plots was constant across communities so that contamination from fertilizer or water treatments due to runoff towards the slough was minimized (Fig. 2). All plots were exclosed using chicken wire (0.5m high, 1.5 cm mesh), preventing grazing by geese. See "Procedure" (below) for treatment details.

Plants to be transplanted came from community 2 ("origin 2 plants") or community 3 ("origin 3 plants"). Four plants of each origin were transplanted into each treatment plot (Fig. 2).

Procedure

Transplant experiment

On 20-27 June, newly emerged arrowgrass plants were excavated along a 100-m stretch parallel to one of the sloughs (at least 100 m from the nearest transect) in community types 2 and 3. All detected plants were excavated, except very small plants because these were expected to have low survival rates. Fresh plants were excavated daily, rinsed in slough water and stored in plastic containers until transplanted. Plants were transplanted to all plots within community 2 first, followed by communities 3, 4, and 1. Plants were individually marked with coloured telephone wire.

Treatments were applied to all plots in a given community type within two days of transplanting. Plots in the fertilizer treatment were fertilized once with a granular 1:1:1 NPK fertilizer (3.6g/m^2 of each element). In light treatment plots, leaves of plants overshadowing arrowgrass were fastened back (where possible) or clipped. Light treatments were repeated where arrowgrass was overshadowed on 7-8 July. Plants in the fresh water plots were supplied with approximately 150 ml/plant of fresh water, while all other plants received an equal quantity of water from the adjacent slough. Water treatments (both fresh and salt) were repeated on 5-6 July and again for communities 2,3, and 4 on 16-18 July.

On 26-28 July, all transplanted plants were excavated, rinsed, transported to Fairbanks, AK, and dried at 60°C for 48 hrs. Plants were washed and redried, divided into leaves, bulbs, roots, and stolons, and weighed. For three randomly selected transects, each group of four replicate plant parts (leaves, bulbs and roots) from a transect/community/treatment/origin combination was pooled to provide samples of approximately 10mg (stolon samples were too small for analysis), which were analyzed for total N (Carlo-Erba Nitrogen Analyzer 1500).

Initial differences between origins

On 22 June 1993, 100 haphazardly located plants were excavated along a 50 m stretch parallel to one of the sloughs in community types 2 and 3 (50 in each), air dried in the field, dried at 60°C for 48 hrs in the laboratory, divided into leaves, bulbs and roots, and weighed.

Environmental Variables and Community Characteristics

On 15-17 June, seven soil samples (25 cm^2 * 5 cm height) were collected along each transect (two each in communities 1, 2, and 3, one in community 4). On 26-28 July, similar samples were collected from two treatment plots (control and fresh water) in each community. All samples were immediately placed in 1400 ml plastic bags and sealed. Samples collected in June were brought to the field laboratory, where water content was determined gravimetrically. Salinity (as $^0/_{00}$ NaCl) was measured on air-dried soils extracted with distilled water (1:2 weight/volume) using a Horiba Cardy saltmeter C-121, and adjusted for initial soil water content. Samples collected on 26-28 July were weighed in the field, air-dried, and brought to Fairbanks where they were dried at 60°C for 48 hrs and processed in the same manner.

On 13-14 July a 0.25m^2 square quadrat divided into 25 10cm*10cm blocks by monofilament was placed on each side of the treatment plots in each community. Plant species located under each of the 16 quadrat crosshairs were identified, percent cover in 16 10cm*10cm blocks per plot was visually estimated, and the height of plants at three points in the quadrat was measured.

Statistical Analyses

Transplant data were analyzed by analysis of variance (ANOVA) where the experimental design was treated as a split-split plot design with four levels: block (transects), whole plot (community), subplot (treatments: fertilizer, water, and light) and sub-subplot (origin) (Table 1; Montgomery 1976). However, because the design contained missing cells (e.g. no light treatment in communities 1 and 2; Fig. 2), it was split into several balanced designs that were analyzed separately. For most effects which did not include light (community, fertilization, water, and their interaction effects), only plots with no light treatment included were used (creating a balanced design with four treatments per community). For calculation of light and light interaction effects,

only control, fertilizer, light, and fertilizerxlight plots in communities 3 and 4 were used. Thus, lightxsalt effects could not be estimated because no light + salt treatment existed. Estimations of effects of origin of plants is based on the use of all data. Where community or interactions effects were significant, pairwise comparisons were performed (starting with the greatest difference and proceeding until differences were not significant) and Bonferroni adjusted probabilities calculated by multiplying the P-value by number of tests performed (Wilkinson 1989).

Mean total nitrogen mass for each pooled group of four plants was calculated as nitrogen concentration multiplied by mean plant weight. Effects of treatment on nitrogen concentration and total plant N mass were analyzed in the same fashion as effects on biomass, but without the sub-subplot (origin) level.

Allocation to plant parts (leaves, bulbs, roots and stolons) was calculated as weight of plant part / total plant weight. Allocation variables were analyzed by ANOVA as for biomass variables. However, allocation to one part is not independent of allocation to other parts. Therefore, for any analysis where effects were significant for at least one allocation variable, we removed the weight of the plant part whose allocation was significantly affected by the treatment (or for which the treatment effect was greatest) from the total weight, and calculated allocation of the other two parts to the remainder (we deleted stolon weight, usually <1% of total weight, for these analyses). We then tested for effects on allocation to the remainder.

Most variables required logarithmic transformation (root and stolon weight, percent root, and all N variables) or inverse logarithmic transformation (leaf, bulb, root, and total weights) to meet model assumptions.

Controlling for plant size

Biomass allocation pattern in arrowgrass changes with plant size (see Results). Therefore, treatments can affect biomass allocation in two ways (Coleman, McConnaughay & Ackerley,

1994): directly (e.g. an increase in allocation to leaves following fertilization because of a shift in C/N balance) or indirectly (e.g. an increase in allocation to leaves following fertilization because fertilized plants are larger than unfertilized plants, and larger plants allocate more to leaves). Because changes in plant size may mask changes in allocation (Coleman et al. 1994), we reran the biomass allocation analyses using total biomass as a covariate for any treatment which resulted in a significant change in total biomass.

Community and Environmental Data

Most early June soil data were analyzed for differences among communities by a one-way ANOVA blocked by transect followed by Tukey's multiple comparison test. Most data from late July were analyzed for community and treatment (water addition) differences by a split-plot ANOVA, with transect at the block level, community at the whole-plot level, and treatment at the subplot level. Because it was not known if the relationship between salinity and water content was linear, salinity data were analyzed using rank-based tests (Kruskal-Wallis for community differences, paired Wilcoxon for the effect of water addition). Differences between communities in vegetation characteristics were analyzed by an ANOVA with transect used as a block, and replicates nested within community. When community effects were significant they were followed by Bonferroni adjusted pairwise comparisons.

RESULTS

Environmental Variables

Soil moisture was consistently higher in early June than in late July, and varied across communities: higher in communities 1 and 4 than in communities 2 and 3 (Table 2). Salinity patterns changed over the course of the season: in early June, salinity was low in communities 1 and 4, and higher in communities 2 and 3, but from June to late July salinity increased in

communities 1 and 2, and decreased in communities 3 and 4. Control and fresh water plots did not differ in soil salinity ($Z = -1.35$, $P>0.1$). Percent cover increased steadily from community 1 to community 4 (Table 2). Communities 1 and 4 were low in species richness and dominated by graminoids (primarily *Carex* species) while communities 2 and 3 were more speciose, with dicotyledons representing a greater percentage of species.

Mortality and Biomass

Overall transplant mortality was 8.1%. Mortality was independent of community ($\chi^2_{(3)} = 4.61$, $P = 0.20$), treatment ($\chi^2_{(6)} = 10.54$, $P = 0.10$), and origin ($\chi^2_{(1)} = 2.3$, $P = 0.13$), but not of transect ($\chi^2_{(9)} = 18.46$, $P = 0.03$).

There was a significant positive relationship between percent allocation to leaves or roots and total biomass (leaves: $t_{(1606)} = 3.72$, $P = 0.0002$; roots: $t_{(1606)} = 4.17$, $P = 0.0001$), and a significant negative relationship between allocation to bulbs or stolons and total biomass (bulbs: $t_{(1606)} = 4.75$, $P = 0.0001$); stolons: $t_{(1606)} = -9.8$, $P<0.0001$).

Community and treatment effects

Communities were significantly different with respect to all biomass variables except root mass (Fig. 3). Total plant mass increased consistently with distance from slough (Fig. 3; overall $F_{(3,27)} = 7.07$, $P = 0.0001$). Allocation to leaves was greater in communities 2, 3 and 4 than in community 1 (overall $F_{(3,27)} = 5.3$, $P = 0.004$). After removing leaf biomass from total biomass, allocation to bulbs versus roots differed between communities ($F_{(3,27)} = 4.96$, $P = 0.007$); bulb allocation decreased more than root allocation did. Allocation to stolons was lower in community

1 than in other communities (after removing leaf weight: $F_{(3,27)} = 6.41$, $P = 0.003$). Controlling for plant size did not change these results.

For all plant parts except stolons, fertilized plants weighed significantly less than unfertilized plants (total biomass: $F_{(1,9)} = 15.7$, $P<0.0001$; Fig. 4). Before controlling for plant size, fertilization had no effect on biomass allocation ($P>0.05$ for all variables), but when total biomass was included as a covariate, fertilization had a significant effect on allocation to bulbs ($F_{(1,9)} = 6.5$, $P = 0.031$). A comparison of the regressions of percent allocation to bulb on total biomass for fertilized and unfertilized plants revealed a lower intercept and steeper negative slope for fertilized plants. This suggests that for a given plant size, fertilized plants allocated less to bulbs than did unfertilized plants. Fertilization did not affect the ratio of leaves to roots ($F_{(1,9)} = 0.007$, $P>0.1$).

Plants to which fresh water was added tended to be larger than those to which salt water was added (22.4 mg vs. 21.5 mg; $F_{(1,9)} = 3.4$, $P = 0.097$). Biomass of plant parts and patterns of biomass allocation did not differ between water treatments.

The light treatment (removing neigbour leaves) did not have a significant effect on the biomass of any plant parts ($P>0.1$ for all variables), but plants in the light treatment had a significantly higher allocation to roots than plants under control light levels (69.2% vs. 67.4%; $F_{(1,9)} = 6.95$, $P = 0.027$). The ratio of leaves to bulbs was not affected ($F_{(1,9)} = 1.54$, $P>0.1$).

There was a significant interaction between community and fertilization for allocation to leaves ($F_{(3,27)} = 3.3$, $P = 0.035$). Unfertilized plants in community 4 had significantly greater allocation to leaves than unfertilized plants in other communities ($F_{(3,27)} = 30.5$, $P<0.0001$), while under fertilized conditions there were no significant community differences. In community 4 fertilization resulted in a significant decrease in allocation to leaves compared to unfertilized plants ($F_{(1,9)} = 7.06$, $P = 0.026$); in other communities there was no difference between fertilized and unfertilized plants.

The fertilizer by light interaction was significant for total biomass ($F_{(2,18)} = 11.34$, $P = 0.0007$), leaf biomass ($F_{(2,18)} = 4.40$, $P = 0.028$), bulb biomass ($F_{(2,18)} = 3.90$, $P = 0.039$), and stolon biomass ($F_{(2,18)} = 3.78$, $P = 0.043$). Under control (low) light levels, fertilization significantly decreased total plant weight, leaf weight, bulb weight and stolon weight ($P<0.05$ for all variables), while under higher light there were no significant differences between fertilized and unfertilized plants ($P>0.1$ for all variables).

Origin effects

Plants originating in community 3 ("origin 3 plants") had significantly greater initial (pre-transplant) bulb weight (7.0mg vs. 4.4mg; $F_{(1,98)} = 20.13$, $P = 0.0002$) greater initial root weight (2.1mg vs 1.5mg; $F_{(1,98)} = 9.35$, $P = 0.003$), and greater initial total weight (13.6 mg vs 9.9 mg; $F_{(1,98)} = 17.97$, $P = 0.0005$) than origin 2 plants. Initial allocation to leaves was greater in origin 2 plants than in origin 3 plants (38.6% vs 34.1%; $F_{(1,98)} = 5.30$, $P = 0.023$), but ratio of roots to bulbs did not differ ($F_{(1,98)} = 0.2$, $P>0.1$).

There were significant post-transplant differences between origin 2 and origin 3 plants for all weight variables except stolon biomass, and leaf allocation (Fig. 5). Origin also had a significant effect on allocation to bulbs versus roots ($F_{(1,9)} = 29.09$, $P = 0.0004$). Origin 3 plants had significantly greater bulb weight and bulb allocation but lower leaf and root weights and leaf allocation than did origin 2 plants, and patterns were the same after controlling for plant size.

There was a significant interaction between fertilization and origin for stolon weight and allocation only. For origin 2 plants, fertilization had a significant negative effect on stolon weight ($F_{(1,9)} = 20.6$, $P = 0.0014$) and allocation to stolons ($F_{(1,9)} = 11.7$, $P = 0.0076$), while there was no significant difference for origin 3 plants between fertilized and unfertilized plants ($P>0.1$).

Nitrogen Concentration and Total Plant Nitrogen

In late July 1992 arrowgrass leaves had a significantly higher N concentration than bulbs or roots (2.36% for leaves vs. 1.84% for bulbs and 1.77% for roots; $F_{(2,374)} = 37.6$, $P = 0.00001$).

Leaf and root N concentration were lowest in community 1 (range: 1.32-2.87% and 1.19-2.52% respectively), intermediate in communities 2 (1.33-3.58% and 0.95-2.67%) and 3 (1.05-3.64% and 1.10-2.22%), and highest in community 4 (1.37-4.22% and 1.37-2.76%), but differences were not statistically significant ($P>0.1$ for both leaves and roots). Total leaf nitrogen mass was significantly greater in community 3 than in community 1 ($F_{(1,2)} = 30.41$, $P = 0.031$). Bulb N concentration was significantly greater in communities 2 and 4 than in community 1 (overall $F_{(3,6)} = 9.81$, $P = 0.01$). Total bulb N was significantly greater in community 4 (2.11%) than in communities 1 (1.58%) and 2 (1.76%; overall $F_{(3,6)} = 8.06$, $P = 0.016$).

Fertilization had no significant effect on N concentration for any plant part ($P>0.1$), but total leaf N was marginally greater for fertilized plants than for unfertilized plants (unfertilized: 1.19 mg; fertilized: 1.40 mg; $F_{(1,2)} = 15.37$, $P = 0.059$).

Fresh water addition had no significant effect on N concentration for any plant part ($P>0.1$), but total root N was significantly greater for plants with fresh water added (0.74mg) than for plants with salt water added (0.65mg) ($F_{(1,2)} = 104.7$, $P = 0.009$). The light treatment had no significant effect on N concentration or total N mass for any plant part. There were no significant differences between origins in N concentration or total N ($P>0.1$).

DISCUSSION

Treatment Effects

Although both addition of nutrients and reduction of competition for light had some effect on plant size and allocation, it is their interaction which produced the most intriguing results. Fertilization resulted in smaller plants and lower allocation to bulbs for a given plant size in all communities, but in the lower levee and wet *Carex* meadow the size effects disappeared when competition for light was reduced. The reduction of light competition by itself only increased allocation to roots. The negative effect of fertilization on arrowgrass may be the consequence of increased growth of neigbouring plants, resulting in greater competition for light. However, even with additional light, fertilized plants were not larger than unfertilized plants, implying that other factors such as increased below-ground competition play a role in limiting plant size.

An alternative explanation for our data is that fertilization did not increase nitrogen availability because of increased immobilization by soil microbes previously limited by P. However, the addition of nutrients affected arrowgrass size, biomass allocation patterns, and increased total leaf N in all communities, and interacted with the light treatments in two communities. In addition, in a previous experiment graminoids in the *Carex* community increased in productivity under the same fertilization scheme (R. Ruess, unpublished data). These results indicate that at least some components of the vegetation experienced an increase in nutrient availability.

The addition of fresh water had a highly significant effect on total root N mass, but no effect on total biomass or allocation pattern. This may be due in part to the limitations of our experimental design. If nutrients are the most limiting factor under unfertilized conditions, and light becomes limiting upon fertilization because of increased shading by neighbours, then any positive effect of fresh water addition on biomass or allocation may only be visible in the fertilizer+light+fresh water treatment. However, because the treatments were not applied in a full

factorial design, we could not estimate the three-way interaction. An alternative hypothesis is that the weak response to water treatments was due to our inability to significantly affect soil salinity: logistical constraints allowed only the addition of a small amount of water to plants, and it rained almost daily during most of the experimental period. We expected the greatest response to water treatments in community 1, but water additions were the least effective there because of runoff on the steep slopes and saturated soils. Salinity could however limit plant growth in drier years, or at a different stage of development (e.g. bulbs).

Community Differences: Limits on Arrowgrass Distribution

Plants did poorly on the slough margin (community 1): they were the smallest, had the lowest allocation to stolons (even though, in general, small plants allocated more to stolons), and had the lowest nitrogen concentrations and total plant nitrogen values. Low allocation to leaves suggests that light competition is relatively unimportant in this community. Community 1 had the most waterlogged soils, which may have lead to lower redox potential (Howes et al. 1981; Adam 1990) and inhibited soil decomposition processes and reduced plant uptake and transport of macronutrients (Drew & Sisworo 1977, 1979; Schat 1980). Although these data suggest that arrowgrass is excluded from this community by low nutrient availability, fertilization did not result in increased plant size. Interspecific competition for light is likely low in this community (as evidenced by low allocation to leaves) even under fertilization. The physical environment, including high soil salinity in July, waterlogging, and flooding (which results in changes in temperature and photoperiod, sedimentation, and damage through effects of currents; Adam, 1990), likely excludes arrowgrass from the slough.

Our data do not explain entirely why arrowgrass is rarely found in the *Carex* wet meadow habitat (community 4) but is common on the lower slough levee (community 3). There were no significant differences in size or plant nitrogen content between community 3 and community 4

plants, but higher percent cover of other species and significantly higher allocation to leaves under unfertilized conditions in the *Carex* meadow suggest that competition for light is greater in this community than elsewhere. Under fertilization, however, allocation to leaves decreased in the *Carex* meadow (but not on the lower slough levee). One explanation is that allocation to leaves had been maximized in the *Carex* meadow prior to fertilization, and that under high competition for light an increase in allocation to bulbs at the expense of leaves and roots allows for early vegetative reproduction or regrowth following grazing. However, without information on the relationship between allocation and future reproduction we cannot interpret these differences.

Differences between Origins

Plants which originated in the lower slough levee (origin 3 plants) had greater bulb weights and allocation, at the expense of leaves, than plants which originated in the upper slough levee (origin 2 plants). The pattern of differences was similar to that of the pre-transplant differences, and the greater overall size for origin 3 plants is consistent with the larger size for all community 3 plants. Differences in allocation patterns between origins could reflect phenological differences between plants in the two communities if the lower slough levee (community 3) becomes snow free at a later date. Stolon weight and allocation were more negatively affected by fertilization in origin 2 plants than in origin 3 plants. If upper slough levee plants are less well adapted to low light environments than lower slough levee plants, an increase in competition for light following fertilization would have a greater negative effect. Alternatively, the difference may again be related to phenology: if fertilization slows down senescence, this may have a greater effect on plants at a later developmental stage (origin 2) than on plants at an earlier stage (origin 3).

Implications for the Role of Herbivory by Geese

In other salt marsh communities, where geese maintain rapidly growing grazing lawns, fertilization by geese has a positive effect on productivity and quality of forage species due to increased nitrogen cycling (Cargill & Jefferies 1984b; Bazely & Jefferies 1985; Ruess et al. 1989; Hik & Jefferies 1990). Our data indicate that in a community in which the preferred forage species is small relative to other species and represents only a tiny portion of the biomass, fertilization may have an overall negative effect on individuals of this species through an increase in interspecific light competition. Our experiments provide two predictions for indirect effects of geese on arrowgrass growth: 1) increased nutrient availability through fecal deposition will have a negative effect because of increased competition for light (and potentially nutrients) by neighbors; and 2) the overall effect of geese will depend on the relative change in nutrient availability versus change in light availability. This will depend on goose selectivity for arrowgrass: if in addition to consuming arrowgrass, competing species are eaten, the negative effect of fertilization mediated by increased light competition should be reduced. It is important to note that geese are likely to have a greater negative effect on neighbours than we did: we removed only enough biomass to decrease shading, while biomass removal by geese may be sufficient to affect belowground competition. On the other hand, other experiments suggest that the percent cover of some neighbouring plant species is negatively correlated with the probability that an arrowgrass individual is grazed: neighbours may provide some protection from grazing (C. Mulder, unpublished data). We hypothesize that goose forage selectivity is key to understanding the interactive effects of herbivory, plant-plant interactions and abiotic factors on arrowgrass because selectivity can affect both the direction and magnitude of the effects of goose presence on individual growth characteristics, and the likelihood of being grazed.

Goose selectivity for arrowgrass may also help explain the virtual absence of arrowgrass in the *Carex* meadow (community 4). The vegetation of the lower slough levee contains several species which are consumed by geese (including *Puccinellia phryganodes* and *Potentilla egedii*)

while the *Carex* species in community 4 are rarely consumed by geese, although geese travel through this community while moving from one foraging area to the next. This differential selectivity for forage may affect arrowgrass abundance: on the slough levee geese could have both a negative effect on the environment of arrowgrass (through fertilization), and a positive effect (an increase in a light availability through consumption of neighbors), while in the *Carex* wet meadow arrowgrass is selectively grazed under high competition for light, which is exacerbated if fertilization occurs. The increased allocation to storage manifested in community 4 may be particularly important for responding to defoliation under low light levels. Of course, additional light availability in the lower slough levee may also affect other stages of the life cycle, such as bulb emergence and seedling establishment.

Conclusions

Our data support the general findings of previous studies that the lower, sea-side (or low-resource) boundary of the distribution of salt-marsh species is limited by physical factors, and the inland (high resource) end by biotic interactions. The slough-side boundary of arrowgrass distribution appears to be limited by physical factors such as flooding and waterlogging, although low nutrient availability may play a role. The absence of arrowgrass in the *Carex* wet meadow may be due to light limitation under fertilization in a habitat where geese selectively remove arrowgrass and increase nutrient availability but not light availability.

Three testable hypotheses regarding the effects of goose presence on arrowgrass emerge from this study: 1) fertilization by geese by itself will have a negative effect on arrowgrass; 2) this negative effect is ameliorated by consumption of neighbors; and 3) the combination of high light competition and high selectivity for arrowgrass limit the expansion of arrowgrass into the *Carex* meadow. The data indicate that future studies should focus on the role of goose selectivity for arrowgrass, and that additional information is needed on the importance of light and nutrient

availability on other stages of the life cycle, as well as on the relationship between allocation patterns and future reproduction.

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Table 1: ANOVA table for the split-split plot analysis (light treatments excluded). Transect is a random variable; all other variables are fixed.

Level / source of variation	d.f.	SS	MS	F
Whole plot				
Transect	10-1	SS_T	$SS_T/9$	
Community	4-1	SS_C	$SS_C/3$	MS_C/MS_{T*C}
Transect*Community	(10-1)*(4-1)	SS_{T*C}	$SS_{T*C}/27$	
Subplot				
Fertilizer	2-1	SS_F	$SS_F/1$	MS_F/MS_{T*F}
Water	2-1	SS_W	$SS_W/1$	MS_W/MS_{T*W}
Fertilizer*Water	(2-1)*(2-1)	SS_{F*W}	$SS_{F*W}/1$	MS_{F*W}/MS_{T*F*W}
Transect*Fertilizer	(10-1)*(2-1)	SS_{T*F}	$SS_{T*F}/9$	
Transect*Water	(10-1)*(2-1)	SS_{T*W}	$SS_{T*W}/9$	
Transect*Fertilizer*Water	(10-1)*(2-1)*(2-1)	SS_{T*F*W}	$SS_{T*F*W}/9$	
Plot by Subplot				
Community*Fertilizer	(4-1)*(2-1)	SS_{C*F}	$SS_{C*F}/6$	MS_{C*F}/MS_{T*C*F}
Community*Water	(4-1)*(2-1)	SS_{C*W}	$SS_{C*W}/6$	MS_{C*W}/MS_{T*C*W}
Transect*Community*Fertilization	(10-1)*(4-1)*(2-1)	SS_{T*C*F}	$SS_{T*C*F}/27$	
Transect*Community*Water	(10-1)*(4-1)*(2-1)	SS_{T*C*W}	$SS_{T*C*W}/27$	
Sub-subplot				
Origin	(2-1)	SS_O	$SS_O/1$	MS_O/MS_{T*O}
Transect*Origin	(10-1)*(2-1)	SS_{T*O}	$SS_{T*O}/9$	
Sub-subplot by whole plot				
Community*Origin	(4-1)*(2-1)	SS_{C*O}	$SS_{C*O}/3$	MS_{C*O}/MS_{T*C*O}
Transect*Community*Origin	(10-1)*(4-1)*(2-1)	SS_{T*C*O}	$SS_{T*C*O}/27$	
Fertilizer*Origin	(2-1)*(2-1)	SS_{F*O}	$SS_{F*O}/1$	MS_{F*O}/MS_{T*F*O}
Sub-subplot by subplot				
Fertilizer*Origin	(2-1)*(2-1)	SS_{F*O}	$SS_{F*O}/1$	MS_{F*O}/MS_{T*F*O}
Water*Origin	(2-1)*(2-1)	SS_{W*O}	$SS_{W*O}/1$	MS_{W*O}/MS_{T*W*O}
Transect*Fertilizer*Origin	(10-1)*(2-1)*(2-1)	SS_{T*F*O}	$SS_{T*F*O}/9$	

Table 2: Soil and vegetation characteristics (mean ± standard error) of four plant communities studied. Different letters indicate a significant difference within rows at $P = 0.05$.

Variable	Slough margin Community 1	Upper levee Community 2	Lower slough levee Community 3	Carex meadow Community 4
Soil characteristics				
Percent water				
June	49.0 ±1.6^{a}	43.2 ±1.0^{ab}	43.1±1.0^{b}	46.0 ±1.2^{ab}
July	43.8 ±0.8^{ac}	38.0 ±1.1^{b}	42.1 ±1.7^{ab}	45.2 ±1.6^{c}
Salinity (^{0}/oo)				
June	7.1 ±0.6^{a}	11.1 ±1.0^{b}	11.4 ±0.9^{b}	9.2 ±0.8^{ab}
July	18.2 ±2.5^{a}	14.4 ±2.7^{ab}	6.8 ±1.0^{b}	8.2 ±1.4^{b}
Vegetation characteristics (July 13-14)				
Percent cover	49.9 ±5.6^{a}	67.3 ±2.7^{b}	77.3 ±3.1^{bc}	85.3 ±1.7^{c}
% Graminoids	97.2 ±0.9^{a}	51.6 ±3.1^{b}	64.4 ±3.0^{c}	85.6 ±1.2^{d}
# Species	1.5 ±0.2^{a}	5.4 ±0.3^{b}	5.2 ±0.2^{b}	3.2 ±0.1^{c}
Height	10.7 ±1.4^{a}	6.4 ±0.5^{b}	6.8 ±0.5^{b}	10.7 ±0.5^{a}

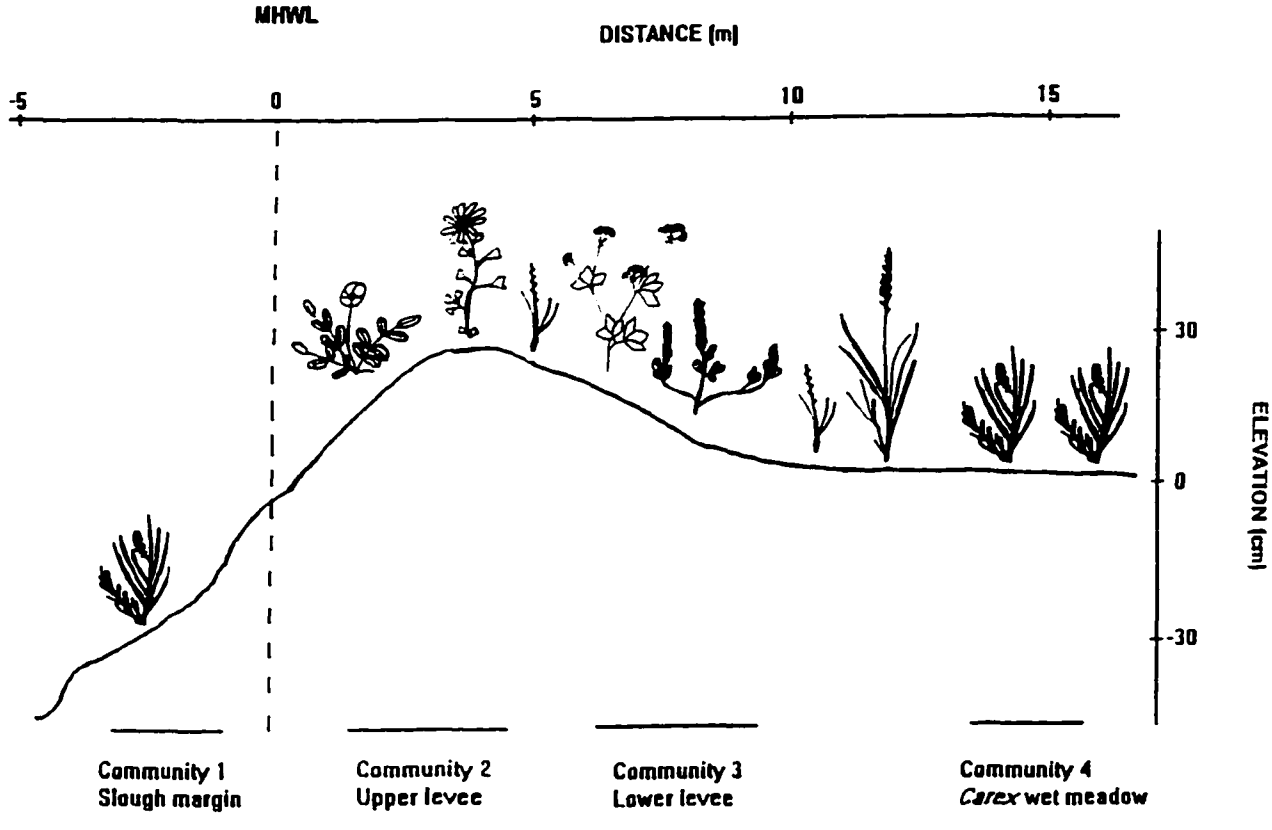

Figure 1. Profile of the slougside plant communities. Elevational data are approximations based on Kincheloe and Stehn (1991). MHWL = Mean High Water Line. Species illustrated (from left to right): *Carex ramenskii / C. glareosa*, *Potentilla egedii*, *Chrysanthemum arcticum*, *Triglochin palustris*, *Ligusticum scoticum*, *Salix ovalifolia*, T. *palustris*, *Elymus arenarius*, C. *ramenskii* / C. *glareosa*.

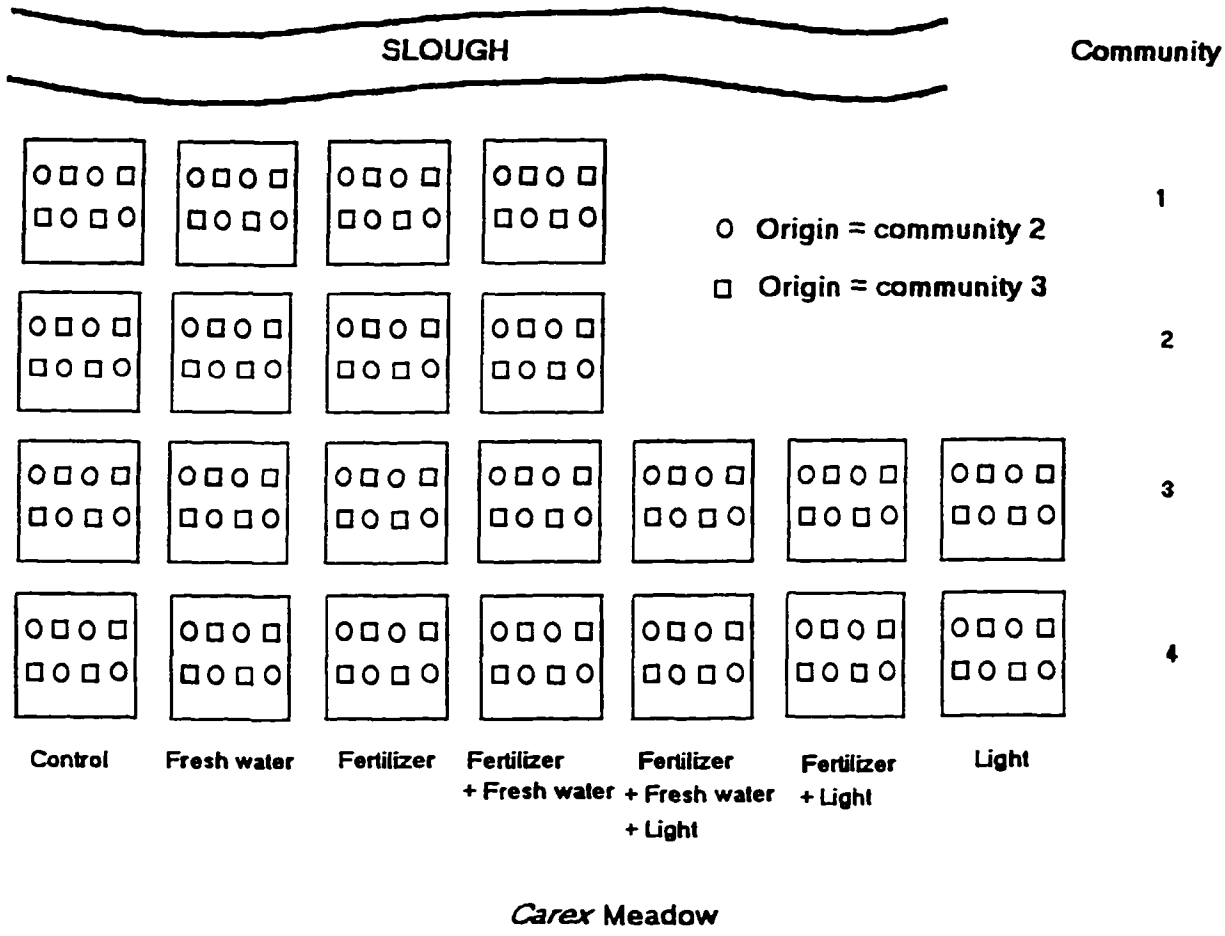

Figure 2. Schematic representation of experimental layout within a transect. This design was replicated ten times.

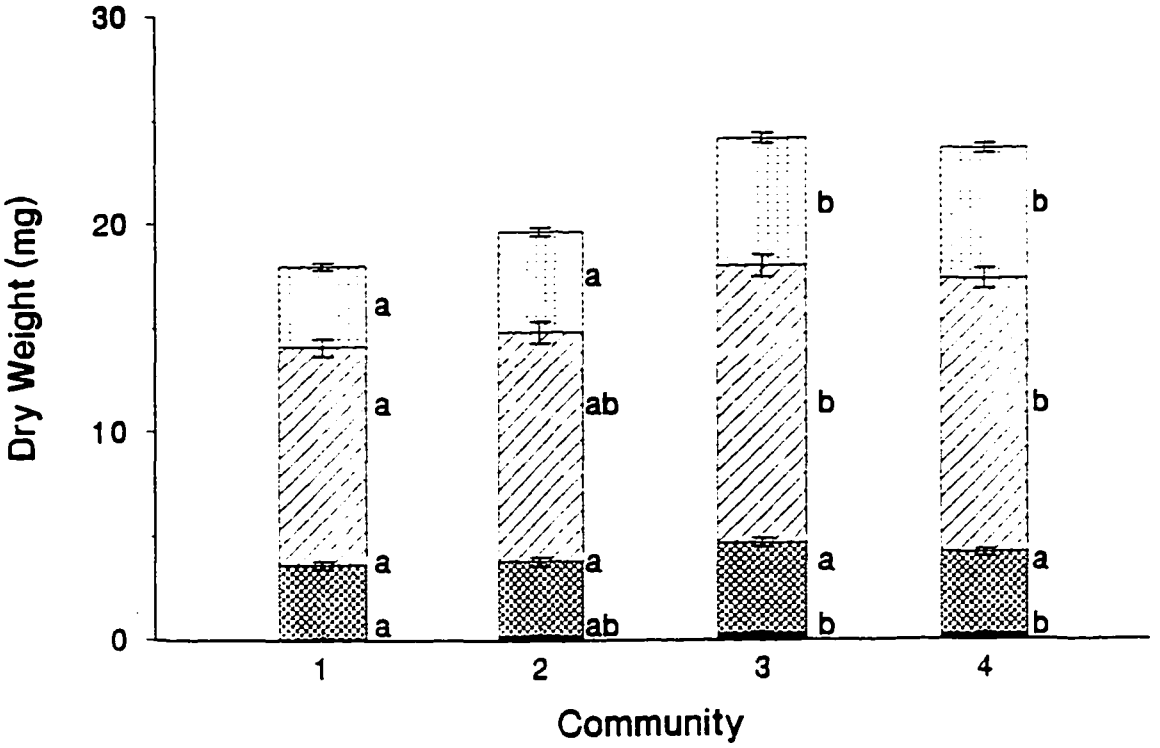

Figure 3. Plant biomass by community. Different letters refer to a significant difference between communities at P = 0.05. Stacked bars (from top to bottom): leaves (stippled), bulbs (hatched), roots (cross-hatched) and stolons (solid).

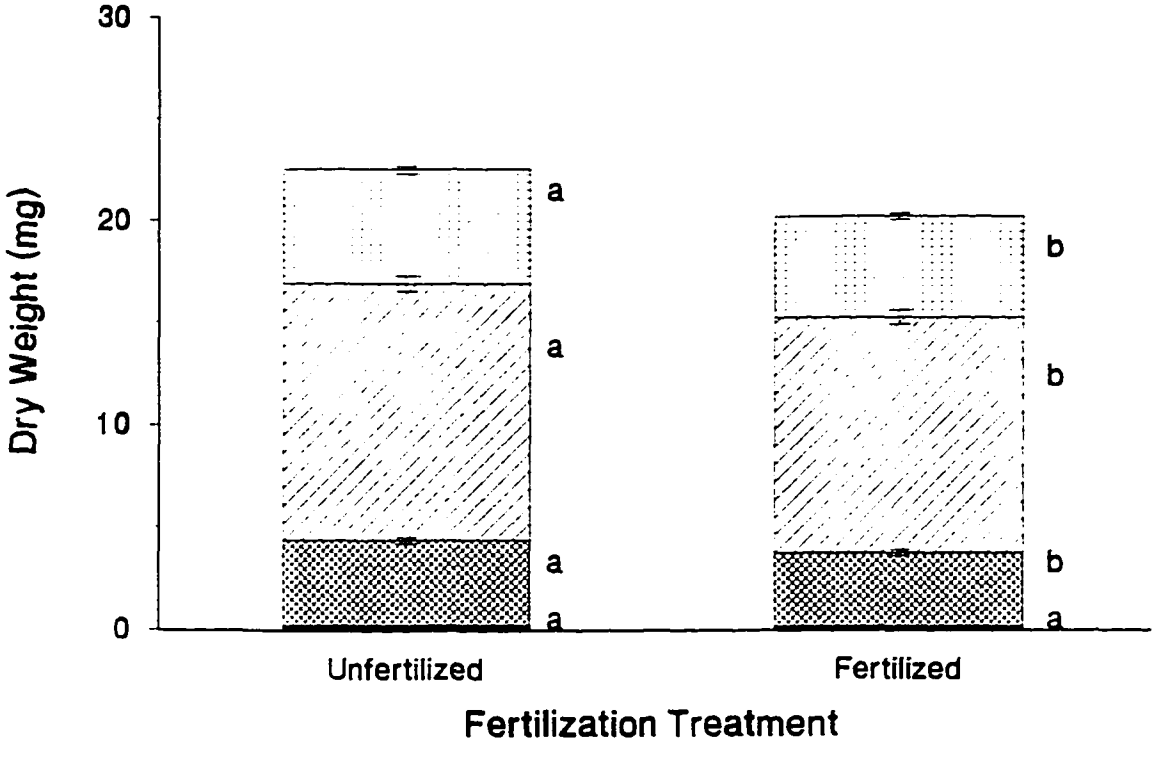

Figure 4. Biomass by fertilization treatment. Different letters refer to a significant difference between treatments at P = 0.05. Stacked bars (from top to bottom): leaves (stippled), bulbs (hatched), roots (cross-hatched) and stolons (solid).

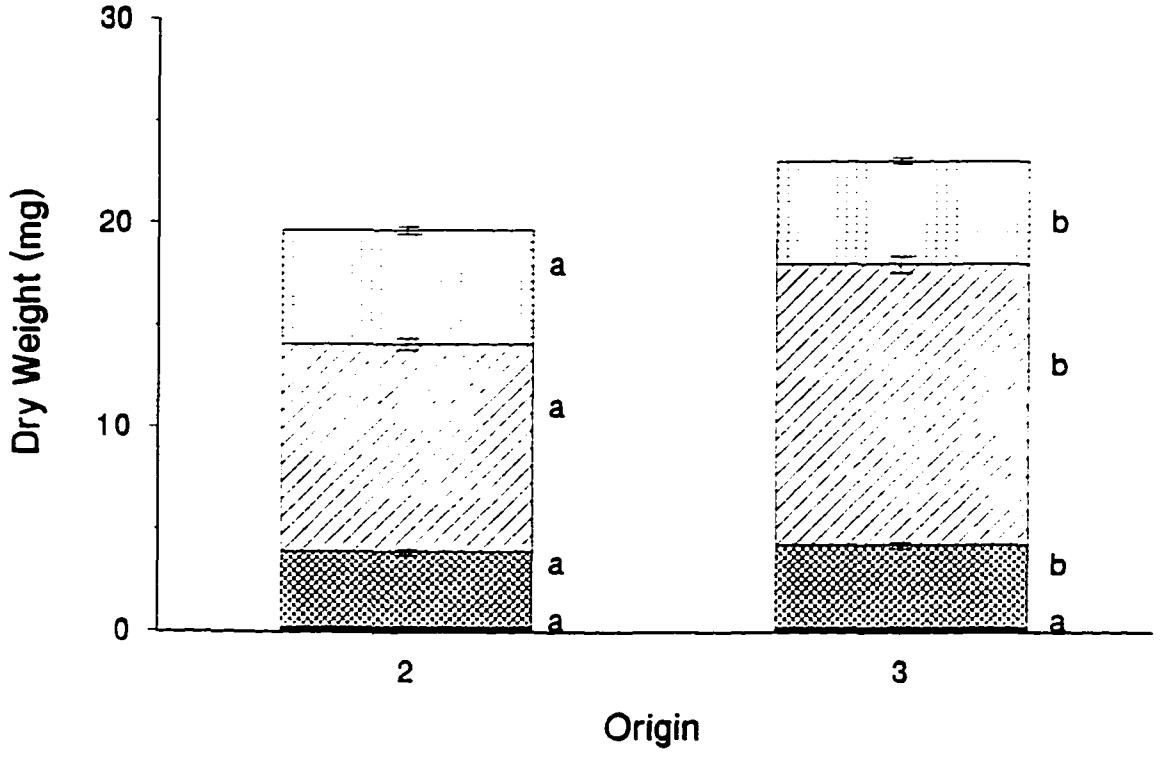

Figure 5. Biomass by plant origin. Different letters refer to a significant difference between origins at P = 0.05. Stacked bars (from top to bottom): leaves (stippled), bulbs (hatched), roots (cross-hatched) and stolons (solid).

CHAPTER THREE:

EFFECTS OF HERBIVORY ON ARROWGRASS: INTERACTIONS BETWEEN GEESE, NEIGHBORING PLANTS, AND ABIOTIC FACTORS[2]

ABSTRACT

Herbivores may affect plants by removing biomass, altering competitive interactions, and altering the abiotic environment, whereas changes in size and quality of forage species and in species composition as a result of herbivory, in turn, affect future herbivory. We investigated the direct and indirect effects of herbivory by brant geese (*Branta bernicla nigricans*) on *Triglochin palustris* (arrowgrass) in a subarctic saltmarsh in SW Alaska. In the first experiment we compared arrowgrass in exclosed plots, unexclosed plots with feces removed, and control plots. In the second experiment, we used a full-factorial design to examine the effects of clipping arrowgrass, clipping neighboring plants, depositing goose feces, and their interactions on arrowgrass size and biomass allocation. In the third experiment, we placed handr-reared goslings on premanipulated plots from the second experiment to examine the effects of arrowgrass size, density, and species composition on probability of an individual arrowgrass being grazed.

For unclipped plants, fertilization resulted in reduced bulb weight, reduced percent biomass in bulb and roots, and increased percent biomass in leaves, whereas fertilization had no effect on clipped plants. Clipping neighbors resulted in increased arrowgrass root weight and stolon weight only for unclipped plants. Feces deposition resulted in increased vegetative reproduction when neighbors were clipped, but had no effect on vegetative reproduction when neighbors were not clipped. Plants in exclosed plots were larger, had greater allocation to leaves, higher concentrations of C and N, and were more likely to flower than plants in unexclosed plots. These results indicate an increase in competition for light with neighbor plants under fertilization, which may be ameliorated by biomass removal of neighbors. Our results predict that an increase in

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grazing pressure is not necessarily detrimental to arrowgrass, provided it is accompanied by increases in comsumption of neighbor plants.

Number of arrowgrass completely removed was not related to arrowgrass density, but number of plants partially grazed increased with arrowgrass density. Probability that an individual arrowgrass plant was grazed was negatively related to biomass or percent cover of several other species (*Potentilla egedii*, *Chrysanthemum arcticum*, *Carex* spp., *Salix* species). These results suggest that some neighbor species may provide a measure of protection (associational refuge) from herbivory, and that an increase in grazing intensity may have a strong negative effect on arrowgrass populations by reducing this protection and through increased likelihood of consumption of arrowgrass remaining after neighbors are removed. We conclude that the way in which we view neighboring plants (as competitors or potential protectors) affects our predictions regarding effects of changing herbivore populations, and that feedbacks from the plant community to herbivores following grazing should be included in studies that aim to extrapolate effects of herbivory on individuals to the population level.

Key words: Alaska, associational resistance, brant geese, *Branta bernicla nigricans*, biomass allocation, grazing, stoloniforous perennial, selective herbivory, subarctic saltmarsh, *Triglochin palustris*, vegetative reproduction.

Key phrases: Deposition of goose feces; Effects of fertilization through competition for light; Feedbacks from plant community to herbivores; Herbivory in homogeneous vs. heterogeneous environments; Interaction of direct and indirect effects of herbivores; Neighbor plants as protectors vs. competitors; Plant density and probability of grazing; Species composition and probability of grazing.

INTRODUCTION

The ability of a plant to compensate for herbivory is affected by the biotic and abiotic conditions it experiences (e.g. Bryant et al., 1983; Cox and McEvoy, 1983; McNaughton and Chapin, 1985; McNaughton, 1986; Maschinski and Whitham 1989; Rausher and Feeny, 1980). Herbivores can affect plant fitness and population dynamics in several ways: (1) directly, through biomass removal (e.g. Morrow and LaMarche, 1979; Louda, 1984; Crawley, 1989); (2) indirectly, by altering morphological traits which determine competitive ability (e.g. Dirzo and Harper, 1980; Parker and Salzman, 1985; Cottam, 1986; Louda et al., 1990;) and (3) indirectly, by altering the environment the plant experiences (e.g. Bazely and Jefferies, 1985, 1986; Huntly and Inouye, 1988; McNaughton et al., 1988; Pastor et al., 1988; Ruess et al., 1989; Whicker and Detling, 1988; Prins and Nell, 1990; Srivastava and Jefferies, 1996). Herbivory often is selective (e.g. Crawley, 1983, 1989; Archer and Detling, 1984; Kinsman and Platt, 1984; Sedinger and Raveling, 1984; Ingham and Detling, 1986; Pastor and Naiman, 1992; Brown and Stuth, 1993), which makes it difficult to extrapolate from responses of individual plants to effects at the community level (Brown and Stuth, 1993). The effect of herbivory on particular species of plant should depend on differential effects on competing species (Fox and Morrow, 1986) and ability of competitors to respond to changes in the resource environment; the effect of herbivory on competition between plants should be greatest when the environment severely limits the opportunities for compensatory regrowth in the consumed species (Louda et al., 1990).

One system in which we may expect to find strong interactions between direct and indirect effects of herbivory is in subarctic salt marshes. Plants in subarctic saltmarshes face a number of stress factors (Adam, 1990), including high or variable soil salinity, waterlogged soils, flooding,

and, in some areas, high levels of herbivory by geese (Cargill and Jefferies, 1984a; Bazely and Jefferies, 1985; Prevett et al., 1985; Gauthier et al., 1995). In addition, arctic and subarctic soils frequently have low availability of nitrogen due to low rates of mineralization and decomposition (Cargill and Jefferies, 1984a; Nadelhoffer et al., 199; Kielland and Chapin, 1992). Geese are may have large effects on community and ecosystem processes in subarctic saltmarshes (e.g. Bazely and Jefferies 1986, 1989; Cargill and Jefferies 1984b; Ruess et al., 1989; Kerbes et al., 1990; Bélanger and Bédard, 1994). Geese can increase rates of nutrient cycling (Cargill and Jefferies, 1984b; Bazely and Jefferies, 1985, 1980; Ruess et al., 1989), raise soil salinity (Srivastava and Jefferies,1996), affect net above-ground primary productivity (NAPP; Cargill and Jefferies, 1984b; Hik and Jefferies 1990), and change species composition and successional rates (Bazely and Jefferies, 1986; Hik et al., 1992). Most studies of goose herbivory in subarctic systems have concentrated on relatively homogeneous 'grazing lawns', but in many other communities, geese are highly selective foragers (Thomas and Prevett, 1986; Sedinger and Raveling, 1984; Prevett et al., 1985; Prins and Ydenberg, 1985) and their preferred forage species are not always dominant. Recently, a number of studies have shown that competition and facilitation play a major role in the structuring of salt-marsh communities (Snow and Vince, 1984; Bertness and Ellison, 1987; Ellison, 1987; Bertness, 1992; Pennings and Callaway, 1992; Bertness and Shumway 1993; Bertness and Hacker, 1994; Castellanos et al., 1994), but it is not well understood how herbivory, abiotic factors, and interspecific interactions combine to affect establishment and growth of individual salt-marsh plants.

We examined the effect of herbivory by geese in a on *Triglochin palustris* L. (arrowgrass; Juncaginaceae), a small, stoloniforous perennial plant, in a subarctic saltmarsh. The study had two principal goals: (1) to test for direct and indirect effects of goose herbivory, including selective

foraging, on growth, abundance and distribution of arrowgrass; and (2) to examine whether a changes in the plant community, as a result of goose presence, altered the probability that an individual arrowgrass was grazed. The latter could simply result from changes in individual or population characteristics of arrowgrass such as plant size, nutrient content, abundance, or distribution. A change in species composition of the community could, however, also alter the probability of consumption of an individual arrowgrass by providing an associational refuge, either by reducing the rate at which herbivores encounter their prey items, by lowering the plant's "visibility" or attractiveness (Atsatt and O'Dowd, 1976; O'Dowd and Williamson, 1979; Hay, 1986), or by increasing availability of alternative food sources (Atsatt and O'Dowd, 1976; Prins and Nell, 1990). Because of the potential for other plant species to provide protection from grazing and thus interact positively with arrowgrass, we will refer to them as "neighbors" rather than as "competitors".

We investigated direct effects of herbivory (biomass removal of arrowgrass), indirect effects (biomass removal of neighbors and changes in nutrient status), and interactions between direct and indirect effects on the performance of arrowgrass by testing two sets of hypotheses generated from previous experiments and observations (Mulder et al., 1996).

Set one: the effect of geese on individual arrowgrass:

1. *Deposition of goose feces results in smaller plants, greater percent biomass in leaves, and lower percent biomass in bulbs.*
2. *Feces deposition will have a greater negative effect on ungrazed arrowgrass than on grazed arrowgrass.*

3. *Effect of feces deposition will be less negative when aboveground biomass of neighbors is simultaneously reduced, whereas the effect of neighbor biomass removal on arrowgrass will be more positive under fertilization than without fertilization.*
4. *Grazing of neighbors will benefit ungrazed arrowgrass more than grazed arrowgrass, and will result in lower percent biomass in leaves.*

In most communities arrowgrass is primarily nutrient limited, while under fertilization it appears to be primarily light-limited (Mulder et al., 1996). Artificial fertilization results in smaller plants with greater percent biomass in leaves, probably as a result of increased interspecific competition, particularly for light (Mulder et al., 1996). Grazed arrowgrass is expected to be severely light limited, so that increased competition for light following fertilization should not change their competitive environment as much as it would for ungrazed plants. Similarly, ungrazed arrowgrass may be able to reallocate carbon to storage or reproduction when more light is available, while grazed arrowgrass individuals are highly carbon limited and will reallocate carbon to leaves regardless of light environment.

Set two: effect of characterstics of arrowgrass and neighbor species on the probability that an arrowgrass individual will be grazed:

1. *Large arrowgrass are more likely to be grazed than small arrowgrass.*
2. *Arrowgrass with high nitrogen concentrations are more likely to be grazed than arrowgrass with low nitrogen concentrations.*
3. *Arrowgrass density affects the probability of being grazed: where arrowgrass density is high, probability that an individual will be grazed is low.*
4. *As percent cover of other species increases, probability of an arrowgrass individual being grazed decreases.*

5. *As contribution of alternative food sources (other preferred species) to species composition increases, probability of an arrowgrass individual being grazed decreases.*

All of these hypotheses assume that a goose chooses to graze in the patch of interest; it is of course possible that a change in vegetation results in geese bypassing a patch altogether, but we were unable to test that hypothesis.

METHODS

Study system

This study was conducted near the Tutakoke River black brant colony during June and July of 1993 and 1994. The site is located on the Yukon-Kuskokwim (Y-K) Delta (southwestern Alaska; 61° 15'N, 165° 30'W), and encompasses an area of approximately 8 km^2 on both sides of the Tutakoke River. The vegetation is described in detail in Kincheloe and Stehn (1991). The Y-K Delta contains high concentrations of nesting Pacific black brant geese (*Branta bernicla nigricans*) and cackling Canada geese (*B. canadensis minima*).

Arrowgrass is a small perennial herbaceous plant that is a preferred forage species for several species of geese (Sedinger and Raveling, 1984; *personal observation*), but which represents only a minor component of the biomass on the Y-K Delta (Mulder et al., 1996). Arrowgrass has a high protein and low fiber content (Sedinger and Raveling 1984; Thomas and Prevett 1986), and it is of particular importance to goslings with growth rates limited by protein; 44-98% of the diet of cackling Canada goslings prior to fledging may consist of arrowgrass (Sedinger 1984; Sedinger and Raveling 1984).

Arrowgrass grows on slough levees and along the edges of small ponds ("slough levee habitat"). This habitat contains a mixture of species including gramnoids (e.g. *Carex ramenskii*,

Elymus arenarius, *Deschampsia caespitosa*), herbaceous species (e.g. *Potentilla egedii*, *Stellaria humifusa*), and several species of dwarf willow. Slough levee habitat borders on mudflat habitat (containing primarily *Carex subspathacea* and *Puccinelia phryganodes*) on the sea-side end, and on *Carex* wet meadows (dominated by *C. ramenskii* and *C. glareosa*) on the upland end. Arrowgrass is a stoloniforous perennial that in this habitat is small (usually 3-15 cm high, <40 mg dry mass) and seldom reproduces sexually (*personal observation*). Arrowgrass produces new bulbs during the growing season, but these do not normally emerge until the following spring (*personal observation*). At the end of the growing season the plant produces a new bulb directly above the bulb of the previous year (*personal observation*). Arrowgrass initiates summer growth at least one week later than the dominant graminoid species(*personal observation*); it started emerging during the 1st days of June in both 1993 and 1994. This species is short compared with most of the surrounding vegetation (mean height in mid July 1994 = 3.7 cm), and where it is abundant it comprises only approximately 4% of aboveground biomass (*unpublished data*). This small size simplifies the interpretation of interspecific interactions; neighbors can affect resources available to arrowgrass, but the effect of arrowgrass on growth of neighbors probably is insignificant, and unlikely to result in a change in competitive ability of neighbors (Goldberg, 1990).

Brant and cackling Canada geese forage in the slough-levee habitat during the later stages of brood rearing (*personal observation*). They consume the above-ground portions of arrowgrass only, although the much less numerous emperor and whitefronted geese also may grub for bulbs before above-ground growth has begun (Budeau et al., 1992).

Experimental design

We conducted three experiments: the "grazing experiment," the "clipping experiment," and the "gosling experiment." Goals of the grazing experiment were: (1) to evaluate the overall effect of the presence of geese and feces deposition on arrowgrass biomass allocation, abundance and distribution; and (2) to understand relationships between the intensity of grazing pressure and characteristics of plant growth. The grazing experiment involved a blocked design with three treatments per spatially separated block: a plot from which geese were excluded (EXCLOSE), an unexclosed plot from which feces were removed (REMOVE), and an unexclosed plot (CONTROL). This design was replicated nine times. The "triplets" (sets of three plots) experienced a wide range of grazing pressures, so that a relationship between grazing pressure and the effect of interest could be established.

The clipping experiment was designed to evaluate the importance of three aspects of goose presence (removal of arrowgrass biomass, removal of neighbor biomass, and fecal deposition), and particularly their interactions, in controlling biomass allocation, abundance and distribution of arrowgrass. This experiment consisted of enclosed plots ("single" plots) subjected to twelve treatments in a 3*2*2 full-factorial design: three levels of feces deposition (none: FECES = 0, a single load: FECES = 1, and a double load: FECES = 2), two levels of arrowgrass clipping (not clipped: AGCLIP = 0 and clipped: AGCLIP = 1), and two levels of neighbor clipping (not clipped: NBCLIP = 0, and clipped: NBCLIP = 1). The single load of feces represented the high end of the natural range of feces deposition, whereas the double load contained more feces than would normally be deposited naturally. This design was replicated three times

In the "gosling experiment" we investigated the effect of changes in species composition on the probability that arrowgrass was grazed by placing captive black brant goslings on the premanipulated clipping experiment plots at the end of the second field season. We chose manipulated plots rather than plots under a natural range of grazing intensities because under natural conditions correlations are likely to already exist between the size of the forage species, species composition, and forage quality (Ward and Saltz, 1994). For example, a heavily grazed plot may have a high percent bare ground and contain a few small arrowgrass with high nutrient content. These correlations make it difficult to separate causal factors. By manipulating forage species size, forage quality, and species composition independently we diminished this problem.

Procedure

Plot set-up

Plots were distributed over an area of approximately 4 km^2 on both sides of the Tutakoke river on 5-8 June, 1994. At this time arrowgrass was 1-2 cm high at most locations. Because arrowgrass distribution across the marsh was patchy, we selected nine general areas based on availability of arrowgrass, grazing pressure (a range from low to high), and accessibility. In each area, one triplet (for the grazing experiment) and four single plots (for the clipping experiment) were set up. The triplets consisted of three adjacent plots spaced 0.5 m apart. Four single plots were placed within 150 m of each triplet, at least 20 m apart. EXCLOSE, REMOVE, and CONTROL treatments were randomly assigned to plots within each triplet, whereas manipulative treatments were randomly assigned to plots across all areas (i.e., not blocked by area). All plots were 1.5 m by 1.5 m and geese were exclosed from all clipping experiment plots and EXCLOSE plots by 0.3 m high chicken wire (2.5-cm mesh) and flagging tape crossed over the top of the plots.

Treatments

Treatments were applied four times in 1993 and three times in 1994 (Fig. 1a). Feces were removed at the start of the experiment (9-14 June 1993) from all plots except CONTROL plots. During each treatment period, all feces were removed from the REMOVE plots and counted in the EXCLOSE and CONTROL plots. Collected feces were dried immediately at 50-60°C.

Feces for fecal additions in the clipping experiment were collected from a *Carex subspathacaea* grazing lawn (they were not abundant enough in the slough-levee community). We collected only fresh feces and kept a subsample for determination of dry mass (Fig. 2c). Feces were stored in a plastic bag and applied within 24 hr of collection.

For AGCLIP = 1 plots, we clipped arrowgrass plants individually with scissors at approximately 1-1.5 cm in height, avoiding inflorescences. This treatment removed 50-80% of arrowgrass plant biomass. For NBCLIP = 1 plots, we initially clipped neighbors (all species except arrowgrass) with shears at a height of 3-5 cm and removed the clippings. This avoided simultaneously clipping arrowgrass but also left most of the "understory", primarily *Salix*, intact. Later clippings of neighbors (Fig. 2) were done with scissors at variable heights to avoid clipping arrowgrass.

Measurements

Measurements were conducted four times during 1993 and three times in 1994 (Fig. 2b), and they were, with few exceptions, identical for plots in the clipping and grazing experiments. We excavated 6-12 plants per plot, counted leaves and stolons, classified each leaf as clipped, grazed,

or whole, and measured plant height, length of each leaf, bulb height and width, "stem height" (the length of the non-photosynthetic part of the leaves, a measure of depth of the bulb in the soil) , stolon length, and, on flowering plants, inflorescence height and number of flowers or fruits. In late July 1995, we collected five flowering plants per plot where available, took above-ground measurements on additional flowering plants in the plot (up to 15 plants), and counted and collected seeds from all remaining flowering plants. All plants were dried at 50-60°C for 48 hr in the field laboratory, divided into leaves, roots, bulbs, stolons, fruits and remainder of the inflorescence, and weighed. Additional above-ground measurements (plant height, longest leaf length, clipping or grazing status) were recorded in the field. Plants collected in late July 1994 were transported to Fairbanks and frozen until time of measurement; some plants thawed prematurely, which accounts for the lower sample sizes for that time period.

We estimated arrowgrass abundance and percent plants clipped or grazed by counting clipped or grazed and unclipped arrowgrass in 3-5, 10 cm by 10 cm subplots in each plot. An estimate of distribution and abundance of arrowgrass was obtained for the grazing experiment plots once a year (17 -30 June 1993, 18-22 July 1994) by placing a 1 m by 0.5 m plexiglass board in the corner of each plot, and marking the location of each arrowgrass individual on an acetate sheet. Measures of dispersion were obtained at two scales by randomly sampling each of the acetate maps 40 times using a 5 cm by 5cm quadrat and a 10 cm by 10 cm quadrat, and calculating the mean to variance ratio for the number of plants located in samples for each size quadrat.

Species composition was estimated in two ways. We removed two or three 10 cm by 10 cm by 2 cm subplots from each plot, cut them to 8 cm by 8 cm by 2 cm in the field laboratory, and removed all above-ground biomass. Clippings were sorted (to species for most dicotyledons,

arrowgrass, *Elymus arenarius*, and for *Puccinellia phryganodes* in 1994; to genus for *Salix* and *Carex* ; most grasses were lumped), dried at 50-60°C for 48 hr, and weighed. A visual estimate of percent cover in 5% increments (plus a category for < 5%) was obtained in four adjacent 10 cm by 10 cm blocks at three locations of each plot. In early July, we noticed that arrowgrass had emerged in almost every disturbed spot where a subplot had been removed within 10 days of the disturbance, so we counted emerged arrowgrass and all other newly emerged species in these areas. On CONTROL and REMOVE plots, grazing intensity was estimated by visually estimating the proportion of plants of each species that were grazed in three 10cm*10cm subplots per plot (in early June, late June, and late July in 1993, and in early June in 1994).

Two soil cores (10-cm deep, 5-cm diam.) per plot were obtained at the end of each season (Fig. 2a). Cores were brought to Fairbanks and stored at 5°C until processed. Soil subsamples (50 g wet mass) were placed in 500ml Mason jars at 15°C in the dark for 21 days for determination of rates of net nitrogen mineralization. We measured rate of soil respiration weekly by gas chromotography (Shimadzu 8 A); jars were vented after each measurement. Both unincubated soils (on day 1) and incubated soils (day 22) were extracted with 2N KCL and we used a modified Technicon autoanalyzer to obtain concentration of mineral nitrogen (NH_4^- + NO_3^-). Net nitrogen mineralization was the difference between mineral nitrogen of soils after and before incubations.

We measured depth of thaw at three points per plot in mid-June and early July 1993, and maximum plant height (of any species) for 12 points in a grid (10cm between points) for three areas within each plot on 1-5 July, 1993.

Gosling experiment

For the gosling experiment we used handreared black brant goslings, 6 wk of age, which were accustomed to feeding freely on vegetation similar to that in the plots. A total of four goslings were used on 23 of the 36 clipping experiment plots. Prior to the experiment, all leaves on each arrowgrass in five 10 cm by 10 cm subplots were measured and subplots were marked with two tongue depressors at opposite corners. Three of the four goslings were fasted for a minimum of 15 min and placed on a plot for an adjustment period of 30 s. The behavior of each gosling was noted each minute and classified as foraging (eating or searching for food), drinking, walking (head up), standing, preening, or grubbing (in mud or water bowl, without head tilting). When the cumulative number of "foraging minutes" (feeding or searching for food) for the three goslings reached 28 min, they were removed from the plot. This ensured that the grazing pressure on each plot was identical. Goslings were fasted for 15 mins between plots, and the order in which plots were used was random with respect to previous treatment of the plots. After goslings were removed from the plot, the subplots were removed and brought back to the field laboratory. We counted and measured clipped, grazed, and whole leaves, dried the plants at 50-60°C for 48 hrs, and estimated arrowgrass biomass per plot.

Statistical analysis

All data were analyzed using SAS statistical packages (SAS Institute, 1995, v. 6.1). Where data were available for multiple time periods (e.g. for mass and size of arrowgrass parts), we used a repeated-measures MANOVA (von Ende, 1993) for mid-July and late-July 1993 and 1994 to examine the effect of month, year, and their interactions with the main effects of the clipping and grazing experiments on arrowgrass size and biomass allocation. We then performed

univariate ANOVAs for two time periods (late July 1993 and late July 1994) seperately. For the clipping experiment, we used the full model (FECES, AGCLIP, NBCLIP, and all interactions). For the grazing experiment the ANOVA included triplet (as a blocking variable) and treatment. Significant effects were followed by contrasts between pairs determined *a priori*. Biomass allocation variables (percent mass in leaves, bulbs, roots and stolons) were analyzed by MANOVA for two time periods (late 1993 and late 1994); where significant effects were detected they were followed by univariate ANOVA. Biomass allocation to one plant part is not independent of allocation to other plant parts. Therefore, for any analysis where biomass was significantly different between treatments, we ran a univariate ANOVA on the biomass allocation of the most affected plant part. We then subtracted the weight of that plant part from the total weight, calculated allocation of the remaining plant parts to the new total weight, and performed another ANOVA.

For the gosling experiment, we determined three indices of grazing: proportion of plants completely grazed (1 - # plants remaining / # plants before grazing), proportion of plants partially grazed (# plants partially grazed / # plants before grazing), and total proportion grazed (complete grazing + partial grazing). Complete and partial grazing were expected to be negatively correlated: an increase in complete grazing may be the result of increased ability to locate or preference for arrowgrass, whereas an increase in partial grazing may indicate a switch to a preferred or more visible plant. Both previous counts of arrowgrass and results from this experiment demonstrated that plants were undercounted in the field compared with laboratory conditions, and that undercounting was proportional to density. We therefore applied a correction factor to the counts taken in the field (correct count = initial count * 1.15) and used corrected values in the calculations of both indices. Stepwise regression models using percent biomass or

percent cover of all species as independent variables were performed to identify those species which best explained proportion of plants grazed.

A measure of dispersion was obtained by taking the mean to variance ratio, and this ratio was used in the ANOVA for treatment effect. Significant deviations from random dispersion were detected through comparisons to a Poisson distribution using a χ^2 goodness-of-fit test (Pielou, 1977).

Most data were log-transformed (all mass data, feces counts) or square-root transformed (proportion flowering) to meet model assumptions, but we use untransformed numbers in figures for ease of interpretation.

RESULTS

Comparison of grazing and clipping experiments

In June 1993 and 1994, the arrowgrass clipping treatment resulted in a higher mean proportion of clipped arrowgrass than the mean proportion of plants grazed in control plots, but by July of both years the proportions were similar (Fig. 2a). Proportion of leaves affected was similar throughout the season in both years (Fig. 2b). In 1993, the FECES = 1 treatment resulted in the addition of a greater amount of feces than would normally be experienced, particularly in the early part of the season; cumulative feces mass at the end of the season was approximately two and one-half times that of the mean for grazing plots and similar to that of the most intensely grazed plot (Fig. 2c). Addition of feces in 1994 was within the normal range for natural deposition in 1993, but high compared with 1994 levels of natural deposition. Both grazing levels and feces deposition suggest that grazing plots experienced lower levels of grazing in 1994 than in 1993. The neighbor clipping treatment resulted in a smaller difference in total biomass/m^2 between clipped and

unclipped plots than did grazing (neighbors not clipped - neighbors clipped vs. EXCLOSE - CONTROL: 113g/m^2 vs. 405 g/m^2 in early June; 280g/m^2 vs. 310g/m^2 in early July 1993; 152g/m^2 vs. 197g/m^2 in early July 1994)

Change in plant mass and biomass allocation over time

In both the clipping and grazing experiments, plants differed in mass between months (early July 1993 or 3rd week of June 1994 versus late July 1993 and 1994) and between years. For all plant parts in both experiments, there was a significant month and year effect or a significant month*year interaction. (Fig. 3a,b). Percent biomass in bulbs and roots decreased over the course of the season, whereas percent biomass in leaves and stolons increased (Fig. 3c,d).

Effects of clipping experiment treatments on arrowgrass : individual level

Addition of feces alone had no effect on mass of any plant part for all time periods together ($P > 0.1$ all mass variables). Clipping by itself had no significant effect on mass of any plant part over all time periods ($P > 0.1$), but a significant interaction for root mass between year, month, and clipping occurred (Wilk's $\lambda = 0.83$, $F_{(1,28)} = 5.54$, $P = 0.026$); in early July 1994, root mass in plots where arrowgrass was clipped was significantly greater than where arrowgrass was not clipped (2.29±0.2 vs. 1.71±0.2 mg; $F_{(1,23)} = 8.41$, $P = 0.008$). Biomass allocation of plants (percent of total mass for all plant parts) in late July 1993 was significantly affected by clipping arrowgrass (Wilk's $\lambda = 0.68$, $F_{(3,23)} = 3.61$, $P = 0.029$). Percent biomass in leaves was greater in unclipped plots (45.3±0.2%) than in clipped plots (40.0±1.3%; $F_{(1,25)} = 5.77$, $P = 0.024$), while the reverse was true for bulbs (42.1±1.9% vs. 48.8±1.5%; $F_{(1,25)} = 11.23$, $P = 0.004$). No difference occurred in percent biomass in bulbs and roots for the remainder of biomass (total mass

- leaf biomass; $P > 0.1$). In early June 1994, prior to the first clipping treatment in that year, longest leaf lengths of plants in clipped plots were significantly shorter than those in unclipped plots (2.4±0.1 vs 2.7±0.1; $F_{(1,23)} = 4.49, P = 0.045$). Mean number of live leaves per plant in plots where arrowgrass was clipped , however, was significantly greater than in plots with unclipped arrowgrass at the end of July 1994 (3.0±0.1 vs 3.5±0.1; $F_{(1,20)} = 5.01, P = 0.036$), resulting in no significant difference in total length of leaves (sum of length of all leaves; $P > 0.1$).

Clipping neighbors significantly increased bulb mass and root mass when all time periods were considered simultaneously (bulb mass: $F_{(1,28)} = 4.77, P = 0.037$; root mass: $F_{(1,28)} = 8.40, P = 0.007$), but had no effect on leaf mass ($P>0.05$). In early July 1994, bulb mass in NBCLIP = 1 plots was significantly greater than in NBCLIP = 0 plots (8.4±0.5 vs. 6.6±0.5; $F_{(1,23)} = 4.91, P = 0.036$), whereas root mass and total mass were marginally greater for NBCLIP = 1 than for NBCLIP = 0 plots (root mass: 2.3±0.2 mg vs. 1.7±0.1 mg, $F_{(1,23)} = 3.21, P = 0.086$; total mass: 21.4±2.7 vs. 15.1±1.1, $F_{(1,23)} = 3.57, P = 0.071$). By late July 1994, differences were no longer significant although trends were in the same direction. The effects of clipping neighbors on root and stolon mass were significant only when arrowgrass was not clipped (Fig. 4). In early June 1994, before the first clipping treatments for that year, plants in NBCLIP = 1 plots were significantly shorter than those in NBCLIP = 0 plots (1.3±0.1cm vs 1.7±0.2 cm; $F_{(1,23)} = 4.44, P = 0.046$).

In late July 1993, there was a significant FECES*AGCLIP interaction for bulb mass ($F_{(1,25)} = 6.2, P = 0.007$) and for biomass allocation (Wilk's $\lambda = 0.62, F_{(6,46)} = 2.07, P = 0.076$): for AGCLIP = 0 plots addition of feces resulted in smaller bulbs, increased percent biomass in leaves, and decreased percent biomass in bulbs, while for AGCLIP = 1 plots addition of feces had no effect on bulb mass or allocation (Fig. 5). When leaves were excluded from total mass, percent biomass

among remaining plant parts did not change with addition of feces. In late 1994, percent biomass in roots was not affected by addition of fertilizer when arrowgrass was not clipped, but it decreased with the addition of fertilizer when arrowgrass was clipped ($F_{(2,22)} = 5.85, P = 0.009$; Fig. 5c).

Where neighbors were not clipped, fertilization did not affect stolon mass or length by late July 1994 (Fig. 6a), whereas clipping neighbors caused total stolon mass and length to increase with fertilization (Fig. 6b). Plants in plots that were fertilized and where neighbors were clipped were significantly larger (greater mass for all plant parts) than those in plots which were neither fertilized nor where neighbors had been clipped (total mass: 36.06±6.90 for FECES = 1 & NBCLIP = 1 vs. 25.07±3.0 for FECES = 0 & NBCLIP = 0).

In plots where arrowgrass was clipped, proportion of plants that flowered in 1994 was significantly lower than in plots in which arrowgrass was not clipped (1.85±1.7% vs 0.54±1.07%, $F_{(1,21)} = 8.15, P = 0.009$). No other treatment in the clipping experiment significantly affected proportion of plants flowering ($P>0.1$ for all variables). Among flowering plants, bulb mass and total fruit mass were significantly greater in AGCLIP = 0 plots than in AGCLIP = 1 plots at the end of July 1994 (bulbs: 15.41±1.1 vs 12.10±1.1mg; $F_{(1,18)} = 5.02, P = 0.037$; fruits:16.24±1.1 vs 13.52±1.0g; $F_{(1,18)} = 5.14, P = 0.035$) Total fruit mass was significantly greater in FECES = 1 plots than in FECES = 0 plots ($F_{(1,16)} = 6.73, P = 0.019$). Mean fruit mass of fresh fruits (total fruit mass / number of fruits) also was significantly greater in FECES = 1 plots than in FECES = 0 plots ($F_{(1,23)} = 8.36, P = 0.0082$) and FECES = 2 plots ($F_{(1,23)} = 4.56, P = 0.044$). There was also an AGCLIP*NBCLIP interaction for fruit mass: clipping neighbors resulted in a smaller number of fruits only in plots where arrowgrass was clipped ($F_{(1,16)} = 4.92, P = 0.041$).

Effects of grazing experiment treatments on arrowgrass: individual level

A significant treatment effect over all time periods existed for total mass, and both a treatment effect and a month by treatment interaction for leaf mass and stolon mass were found (Fig. 7). In mid-July, total mass, leaf mass and bulb mass of EXCLOSE plot plants were significantly greater than those of CONTROL and REMOVE plots, but by late July there were no differences among treatments (Fig. 7). Plant biomass allocation was affected by grazing treatments in late July 1994 (Wilk's $\lambda = 0.065$, $F_{(2,8)} = 4.39$, $P = 0.01$), when percent biomass in leaves in the EXCLOSE treatment (43.7±2.4%) was significantly greater than in the CONTROL treatment (38.5±1.7%; $F_{(1,5)} = 8.12$, $P = 0.035$). Longest leaves on plants in early 1994 plants in EXCLOSE plots were significantly longer (2.73±0.1cm) than those in CONTROL plots (2.28±0.1; $F_{(1,13)} = 11.10$, $P = 0.005$), whereas mean leaf length was significantly greater in EXCLOSE than CONTROL ($F_{(1,14)} = 7.86$, $P = 0.014$) or REMOVE plots ($F_{(1,14)} = 8.25$, $P = 0.012$)

In late July 1993, a significant negative relationship between grazing intensity (as measured by number of feces removed from remove plots) and total mass and leaf mass of REMOVE plots occurred (Fig. 8). In late 1994, there was no relationship between 1994 grazing intensity and plant mass in REMOVE plots, but we found a marginally significant positive relationship between grazing intensity in 1993 and total mass ($R^2 = 0.50$, $F_{(1,3)} = 5.07$, $P = 0.11$). Correlation between number of feces removed in 1993 and 1994 (an index of use by geese) was weak ($r = 0.454$, $P = 0.22$). Treatments in the grazing experiment had a significant effect on the proportion of plants flowering: EXCLOSE plots had a significantly higher proportion of

plants flowering (2.1±2.9%) than REMOVE plots (0.02±0.13%; $F_{(1,15)} = 15.18, P = 0.001$) or control plots (0.1±.26%; $F_{(1,15)} = 18.60, P < 0.001$).

Total bulb N was significantly greater in EXCLOSE plots (0.18±0.03 mg) than in CONTROL plots (0.12±.01 mg; $F_{(1,14)} = 8.46, P = 0.011$) or REMOVE plots (0.13±0.01mg; $F_{(1,14)} = 5.76, P = 0.03$). Total bulb carbon also was significantly greater in EXCLOSE plots (2.83±0.3mg) than in CONTROL plots (2.00±0.2mg; $F_{(1,14)} = 10.14, P = 0.007$) or REMOVE plots (1.87±.2mg; $F_{(1,14)} = 9.96, P = 0.007$). There were, however, no differences in nitrogen or carbon concentrations between the treatments ($P>0.05$).

Effects of treatments on arrowgrass: population level

Rate of population growth (# plants in late 1994 / # plants in late 1993) was not significantly affected by clipping experiment treatments. For stolon productivity (total stolon mass / 100 cm^2) in late 1994 a significant interaction between feces addition and clipping neighbors occurred ($F_{(2,15)} = 4.93, P = 0.023$): where neighbors were not clipped, feces addition decreased stolon productivity (1.10 ±0.2 mg versus 3.78±1.2 mg), whereas where neighbors were clipped, feces addition had no effect on stolon productivity.

In the grazing experiment, treatment had no effect on rate of population growth, but it did have a strong significant effect on standing biomass of arrowgrass in early July 1994: standing biomass of arrowgrass in EXCLOSE plots (1.52±0.3g/100cm^2) was greater than in REMOVE plots (1.09±0.2g/100cm^2; $F_{(1,7)} = 19.74, P = 0.003$), while standing biomass of CONTROL plots was intermediate (1.20 ±0.2 g/100cm^2).

Dispersion of arrowgrass was usually significantly clumped or not distinguishable from random; vew plots exhibited a hyperdispersed distribution (Table 1). Although treatments had no

significant effect at any time-scale combination ($P > 0.8$ for all), there were some intriguing patterns (Table 1). For example, four of five plots which showed significant hyperdispersion at some time or scale were control plots. There was a marginally significant relationship between grazing intensity in 1993 (as measured by feces deposition for REMOVE and CONTROL plots) and dispersion at the small scale for both 1993 ($F_{(1,15)} = 3.28, P = 0.09, R^2 = 0.13$) and 1994 ($F_{(1,15)} = 3.98, P = 0.06, r^2 = 0.16$, Fig. 9).

Effects of treatments on community and ecosystem levels

Species composition was too variable between plots and between years to evaluate effects of the clipping and grazing experiments. Maximum height of vegetation (including all species) in the clipping experiment was significantly reduced by clipping neighbors (3.9±0.2 cm vs. 5.7±0.5 cm; ($F_{(1,23)} = 14.6, P = 0.009$). In the grazing experiment vegetation height was significantly greater in EXCLOSE plots (5.5± 0.2 cm) than in CONTROL plots (4.9±0.2 cm; $F_{(1,16)} = 5.16, P = 0.037$) or in REMOVE plots (4.7±0.2 cm; $F_{(1,16)} = 8.47, P = 0.010$). Treatments in the clipping experiment had no effect on rate of net mineralization or on rate of soil respiration ($P > 0.1$ for all variables). The grazing experiment treatment had no significant effect on respiration rate, but there was a significant difference between treatments in rate of net mineralization: net mineralization in REMOVE plots was positive (2.26±.9$\mu gN_{dry\ mass}^{-1}$ day^{-1}) and significantly greater than for CONTROL plots, where it was negative (-0.67±.8$\mu gN_{dry\ mass}^{-1}$ day^{-1}; $F_{(1,15)} = 62.7, P = 0.024$). Change in depth of thaw between mid June and early July 1993 was not significantly affected by any treatment ($P > 0.1$ for all).

Gosling Experiment

Proportion of arrowgrass completely grazed was higher for FECES = 2 plots than for FECES = I plots (38.9±6.7% versus 18.1±4.1%; $F_{(1,12)} = 7.04$, $P = 0.021$). Total proportion grazed was significantly lower in plots where arrowgrass was clipped than where it was not (43.34±6.8 versus 72.2±5.8%; $F_{(1,13)} = 6.58$, $P = 0.024$). There was no effect of the clipping treatments on the proportion of arrowgrass completely grazed ($P > 0.1$ for all treatments).

We conducted stepwise multiple regressions to find the model that best explained proportion of plants grazed by species biomass or percent cover, with eleven candidate species or taxonomic groups (Table 2). In all models (proportion partially grazed, proportion completely grazed, and total proportion grazed), arrowgrass biomass or percent cover were retained in the model (Table 2). Other explanatory variables retained were moss biomass, *Chrysanthemum arcticum* biomass, *Potentilla egedii* biomass, *Carex* percent cover, and *Salix* percent cover (Table 2). No relationship existed between mean vegetation height and proportion of plants completely grazed ($F_{(1,20)} = 2.9$, $P = 0.10$), but there was a negative relationship between mean vegetation height and proportion partially grazed ($F_{(1,20)} = 8.62$, $P = 0.008$, $r^2 = 0.27$).

Proportion of plants completely grazed was affected by arrowgrass characteristics: we found a significant positive relationship between proportion completely grazed and mean total leaf length per plant ($F_{(1,21)} = 4.49$, $P = 0.046$, $r^2 = 0.14$), and a marginal positive relationship for mean number of leaves per plant ($F_{(1,21)} = 4.21$, $P = 0.053$, $r^2 = 0.13$), but none with mean leaf length ($F_{(1,21)} = 1.88$, $P = 0.18$). As expected, a strong negative relationship also existed between proportion of plants completely grazed and the sum of all leaf lengths in the subplots ($F_{(1,21)} = 10.22$, $P = 0.004$, $R^2 = 0.30$). There was a strong negative relationship between the mean number of arrowgrass in the subplots and proportion of plants which were completely grazed: the

higher the plant density, the lower the proportion of plants completely grazed ($F_{(1,21)}$ = 16.05, P = 0.0006, R^2 = 0.41; Fig. 10a; after removal of an outlier, R^2 = 0.28, $F_{(1,20)}$ = 9.20, P = 0.007). Nevertheless, a regression of estimated number of arrowgrass completely grazed versus arrowgrass density was not significant (outlier not included, $F_{(1,20)}$ = 0.12, P = 0.73; Fig. 10b). In other words, number of arrowgrass removed was independent of arrowgrass density. In contrast, the number of remaining arrowgrass partially grazed was strongly related to intial arrowgrass density (R^2 = 0.54, $F_{(1,20)}$ = 25.97, $P < 0.0001$; Fig. 10c): as arrowgrass density increased, so did number of plants partially grazed.

Proportion of plants partially grazed also was affected by arrowgrass characteristics, but often in the opposite direction. A significant negative relationship occurred between proportion of plants partially grazed and mean total leaf length per plant ($F_{(1,21)}$ = 6.20, P = 0.021, R^2 = 0.19), a marginal negative relationship with mean length of leaves ($F_{(1,21)}$ = 3.73, P = 0.067, R^2 = 0.11), and no relationship with mean number of leaves ($F_{(1,21)}$ = 1.67, P = 0.21). We found no relationship between the proportion of plants which were partially grazed and arrowgrass density ($F_{(1,21)}$ = 0.67, P = 0.42) or total sum of all leaf lengths in the subplots ($F_{(1,21)}$ = 0.015, P = 0.91). No relationship existed between nitrogen concentration in leaves and the proportion of plants partially or completely grazed ($P>0.1$)

DISCUSSION

Evaluation of hypotheses regarding effects of geese on arrowgrass

Most of the original hypotheses concerning effects of geese on individual arrowgrass were supported by data from the clipping experiments, although for some the support was limited. The hypotheses that deposition of goose feces results in smaller plants, greater percent biomass in

leaves, lower percent biomass in bulbs, and that the effects would be greater for ungrazed than for grazed arrowgrass were fully supported by the clipping experiment. For unclipped plants only, fertilization resulted in reduced bulb mass, reduced percent biomass in bulbs and roots, and increased percent biomass in leaves, whereas there was no effect of fertilization on clipped plants. These results are consistent with the hypothesis that fertilization stimulates the growth of neighbors, leading to increased competition for light, which in turn results in increased demand for photosynthetic tissue, but that demand cannot be met when plants are severely carbon limited. We expect that although deposition of feces on plants during grazing generally will have a negative effect on arrowgrass, such effects will be less visible for plants that have been grazed. This smaller effect of fertilization on grazed plants may explain some of the results from our grazing experiment: although plants in CONTROL plots tended to be smaller than those in REMOVE plots, differences were not significant, possibly because high feces deposition was associated with high rates of grazing. Fertilization had a positive effect on flowering arrowgrass; the addition of a single load of feces resulted in a greater total mass of fruit. Flowering plants are, however, larger than nonflowering plants, and they may therefore represent those plants that suffered relatively little competition (e.g. because they were in an open location) and therefore experienced only the advantages of fertilization. If this holds, then fertilization may increase the variance in plant size. Addition of a single load of feces also resulted in a greater standing biomass for arrowgrass than either addition of a double load or no feces, which may have resulted from increased percent biomass in leaves.

We observed less support for the hypothesis that the effect of feces deposition would be lessened when above-ground biomass of neighbors was simultaneously reduced. Such an effect was seen only for vegetative reproduction: stolon length and mass increased under fertilization

when neighbors were clipped, but decreased when neighbors were not clipped. The last hypothesis, that the grazing of neighbors would benefit previously ungrazed arrowgrass more than grazed arrowgrass, was partially supported by the clipping experiment. Clipping neighbors resulted in increased root mass and stolon mass only for unclipped arrowgrass, suggesting that for grazed plants, the advantage of simultaneous grazing of neighbors was minimal.

In saltmarsh communities, where geese maintain rapidly growing "grazing lawns," they can greatly increase forage productivity and quality by increasing rate of nitrogen cycling (Cargill and Jefferies, 1984*b*; Bazely and Jefferies, 1985; Ruess et al. 1989; Hik and Jefferies 1990). Our data indicate that such an effect was absent in areas where foraging was selective and the preferred species represent a small proportion of the total biomass. The overall negative effect of the presence of geese seen in the grazing experiments (as evidenced by the greater size, greater C and N mass, and higher probability of flowering in exclosed plots) can be attributed to two factors: direct removal of biomass and an increase in competition for light with neighboring plants following deposition of feces. The clipping experiment indicates that a primary cost to arrowgrass of biomass removal is a decrease in sexual reproduction: clipped plants were less likely to flower (even though we avoided removing inflorescences when clipping), and when clipped plants did flower their bulb mass and total fruit mass were lower than for unclipped flowering plants. Clearly, effects of biomass removal plus fertilization in the presence of geese are more negative than the effects of increased competition for light (through elimination of trampling and herbivory for all species) when geese are absent.

Evaluation of hypotheses regarding effects of arrowgrass and neighbor species characteristics on probability of arrowgrass being grazed

Associational resistance (a reduction in herbivory on one plant species in the presence of another) has been reported in a number of systems, many of them involving specialized insect herbivores (e.g Tahvanainen and Root, 1972; Bach, 1980; Risch, 1980, 1981; Kareiva 1982; Ellison, 1987), but also in some systems involving more generalist, wide-ranging herbivores (e.g. McNaughton, 1978; Hay, 1986). The repellent-plant hypothesis (physical or chemical characteristics of an unpalatable species interfere with the herbivore's ability to find or use the palatable species; McNaughton, 1978; Atsatt and O'Dowd, 1976; Hay, 1986; Ellison, 1987) and the attractant-decoy hypothesis, (other species provide more attractive alternative food sources; Atsatt and O'Dowd, 1976) have both been used to explain this effect. These hypotheses are difficult to test, particularly for noninsect, generalist species, because correlations between rates of herbivory and the presence of other species in natural situations can be the result of both direct and indirect effects of past herbivory (Ward and Saltz, 1994). For example, past herbivory may have increased the palatability of the preferred species and reduced the presence of other palatable species, resulting in a negative correlation between proportion of preferred plants grazed and biomass of other species. We reduced this problem by using pre-manipulated plots in the gosling experiment, in which correlations between arrowgrass size, community composition, and arrowgrass quality (N concentration) had been decreased. Our results indicate that both arrowgrass characteristics and community composition affect probability of arrowgrass being grazed. Plant size was a good indicator of probability of being grazed: proportion of plants completely grazed increased as mean number of leaves increased, whereas plants that had been clipped previously were less likely to be grazed than those which had not been clipped. On the other hand, there was no evidence that plants in plots with a higher mean N concentration were more likely to be grazed. Because we pooled plants per plot to obtain a sample large enough for

analysis, we do not know the within-plot variance in N concentration, which makes it impossible to evaluate the power of our test.

Number of arrowgrass completely removed was unrelated to arrowgrass density, but number of arrowgrass partially removed increased with density, suggesting a change in the effectiveness with which arrowgrass were consumed. Additional species, both palatable and unpalatable to geese, were included in the models explaining proportion grazed, and generally relationships between species presence (biomass or percent cover) and proportion of arrowgrass removed were negative, whereas those with proportion of plants partially grazed were positive. Moss biomass, which is correlated with patches of bare ground, was the exception (*personal observation*), and it therefore appears that in plots with little vegetation, proportion of arrowgrass grazed completely is very high, while the proportion partially grazed declines. *Potentilla egedii* and *Carex* are both potential alternative food sources, whereas dwarf *Salix* species provide good ground cover, suggesting that both increased crypsis and the availability of alternative food sources decrease the probability of arrowgrass being grazed. The significant correlations between proportion of plants partially grazed and biomass or percent cover by other species indicate that changes in the probability of grazing are not simply the result of a shift to other food sources, which should lead to changes in complete grazing only. Thus our data support both the repellent-plant hypothesis and the attractant-decoy hypothesis. The results of this experiment also are consistent with the observation by Sedinger and Raveling's (1984) that arrowgrass is grazed more heavily by cackling Canada geese on the mudflats, where it is surrounded only by very short *Puccinellia phryganodes* and *Carex subspathacea*, than in the mixed-species slough levee communities.

Implications of experimental results for the effects of an increase in grazing intensity

On the Yukon-Kuskokwim Delta, number of nesting pairs of brant geese has steadily increased for the past decade (Sedinger et al., 1993, 1994; Anthony et al. 1995). This increase in goose population should increase grazing intensity and competition for high-quality forage, and potentially increase breadth of diet(Pyke et al., 1977). On the Y-K Delta, cackling Canada geese, which are similar to brant in size and foraging habits (*personal observation*), ate less arrowgrass and more graminoids in years when brood densities were higher, as well as later in brood rearing, when vegetation quality declines (Sedinger and Raveling, 1984). Reduced consumption of arrowgrass also was associated with greater time spent foraging, suggesting greater search times were needed to fill the gut (Sedinger and Raveling, 1988). Predictions regarding the effects of an increase in grazing intensity coupled with a decrease in selectivity will differ depending on whether they are drawn from the clipping and grazing experiments or from the gosling experiment. Results from the clipping experiment suggest that if an increase in grazing pressure is accompanied by an decrease in selectivity, it may initially benefit arrowgrass: plants will be more likely to be grazed, but light availability should increase as neighbors are also consumed so that the overall effect on arrowgass may be neutral. The grazing experiment provides mixed evidence for this hypothesis. In 1993, a negative relationship between grazing intensity and plant mass existed, contradicting our hypothesis. In 1994, however, this relationship was not found, and a slightly positive relationship occurred between 1993 grazing intensity and 1994 plant mass, which is what we would expect if, as is predicted from clipping experiment results, percent biomass in vegetative reproduction in

1993 was greater in heavily grazed plots. Thus, both clipping and grazing experiments suggest that a moderate increase in grazing intensity is not neccesarily detrimental to arrowgrass.

In contrast, the gosling experiment suggests that any increase in grazing pressure accompanied by a decrease in selectivity will exacerbate the negative effects of goose grazing. If the presence of some neighboring species provide arrowgrass with a measure of protection from goose grazing (either by providing alternative foods or by decreasing detection of arrowgrass), greater consumption of neighbors should result in greater probability of arrowgrass being grazed. Plants that have been grazed previously will have shorter leaves, but more of them; this should decrease the probability of partial grazing, but increase the probability of presumably more detrimental complete grazing. Overall, the gosling experiment results points toward a rapid decline in the arrowgrass under increased grazing pressure accompanied by decreased selectivity for arrowgrass by geese.

The effects of increased grazing pressure on arrowgrass populations will depend of course on the relative magnitudes of these different predicted effects. Such effects cannot be estimated without more detailed information on the foraging behavior of geese at both small and large scales when faced with different foraging situations. We need a better understanding of how selectivity changes with goose population size, and how geese select a foraging area also is essential. Although the increase in arrowgrass standing biomass following feces deposition may result in greater attractiveness of previously grazed areas, both observations and feces correlations between 1993 and 1994 suggest that there is little consistency in the specific areas that are grazed. Questions regarding the way in which geese locate arrowgrass within a patch also remain. For example, the grazing experiment provides evidence that goose herbivory results in a decrease in clumping, but it is unclear how this would affect the probability of arrowgrass being grazed.

Conclusions

When we examine results from the clipping and grazing experiments only, weare tempted to conclude that the overall effect of geese on arrowgrass is negative, in part because under increased fertilization arrowgrass is outcompeted for light by its neighbors. Nevertheless, the gosling experiment suggests that the presence of other species also can have a positive effect on arrowgrass. Thus, the way in which we view other species in the system (as competitors or potential protectors) changes the predictions we make regarding the effects of an increase in geese numbers when accompanied by an increase in diet breadth. We cannot predict the net result of these opposing effects; however, they do point out that in examining the effect of herbivory on a plant in the context of a community, we need to focus not just on direct and indirect effects of the herbivore on the plant, but also on feedback from the plant community to the herbivore through changes in forage plant size, forage quality and species composition. Understanding such feedbacks will require the coupling of clipping or controlled grazing experiments with experiments that can independently assess the effects of these factors (plant size, forage quality and species composition) on herbivore behavior, forage preference, and foraging efficiency.

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Table 1: Summary of dispersion data by treatment. Data are for arrowgrass in exclosed plots, control plots, and plots with goose feces removed on the Yukon-Kuskokwim Delta in 1993 and 1994. The dispersion index refers to the mean : variance ratio for map samplings (see text for details), where ratio = 1 indicates a random spatial distribution of plants, ratio > 1 signifies hyperdispersion, and ratio < 1 signifies clumping.

Treatment	Scale /Year	#plots index < 1	#plots index <1 and $P< 0.05$[a]	#plots index >1	#plots index >1 and $P< 0.05$
EXCLOSE	SM/93[b]	8	3	1	0
	LG/93	8	5	1	0
	SM/94	8	1	1	0
	LG/94	8	2	1	1
REMOVE	SM/93	6	5	2	0
	LG/93	6	4	2	0
	SM/94	3	1	5	0
	LG/94	6	4	2	0
CONTROL	SM/93	6	1	3	0
	LG/93	6	1	3	2
	SM/94	7	0	2	1
	LG/94	7	3	2	1

[a] $P<0.05$ refers to plots for which the distribution is significantly different from random as determined by a chi-square goodness-of-fit test when compared to a Poisson distribution with the same mean.
[b] SM and LG refer to small scale and large scale respectively; "93" and "94" refer to 1993 and 1994.

Table 2: Species explaining probability of arrowgrass being grazed: variables retained in a stepwise regression. Data are for plots in late July 1994 on the Yukon-Kuskokwim Delta. Candidate response variables were the aboveground biomass or percent cover of arrowgrass, *Carex* spp., *Elymus arenarius*, *Potentilla egedii*, *Petasites frigidus*, *Chrysanthemum arcticum*, *Stellaria monantha*, *Ligusticum scoticum*, *Salix* spp., *Puccinellia phryganodes*, "other grasses", and moss.

Dependent variable	Independent variable	Parameter Estimate	*t*	*P*[a]
Using species biomass:				
Proportion completely grazed	Arrowgrass	-10.7	-3.58	0.002
	Moss spp.	23.3	1.86	0.077
Proportion partially grazed	Arrowgrass	39.7	3.30	0.004
	Moss spp.	-107.4	-2.14	0.046
	Chrysanthemum	-6.3	-1.86	0.079
Total proportion grazed	Arrowgrass	35.4	2.97	0.008
	Chrysanthemum	-7.1	-2.31	0.032
	Potentilla	-8.0	-2.03	0.057
Using percent cover:				
Proportion completely grazed	Arrowgrass	-0.25	-3.55	0.002
	Salix spp.	-0.01	-2.97	0.008
Proportion partially grazed	*Salix* spp.	0.005	2.88	0.009
Total proportion grazed	Arrowgrass	-0.206	-3.87	0.001
	Carex spp.	-0.017	-2.55	0.020
	Salix spp.	-0.007	-2.42	0.026

[a] Significance level to enter = 0.15; significance level to exit = 0.10

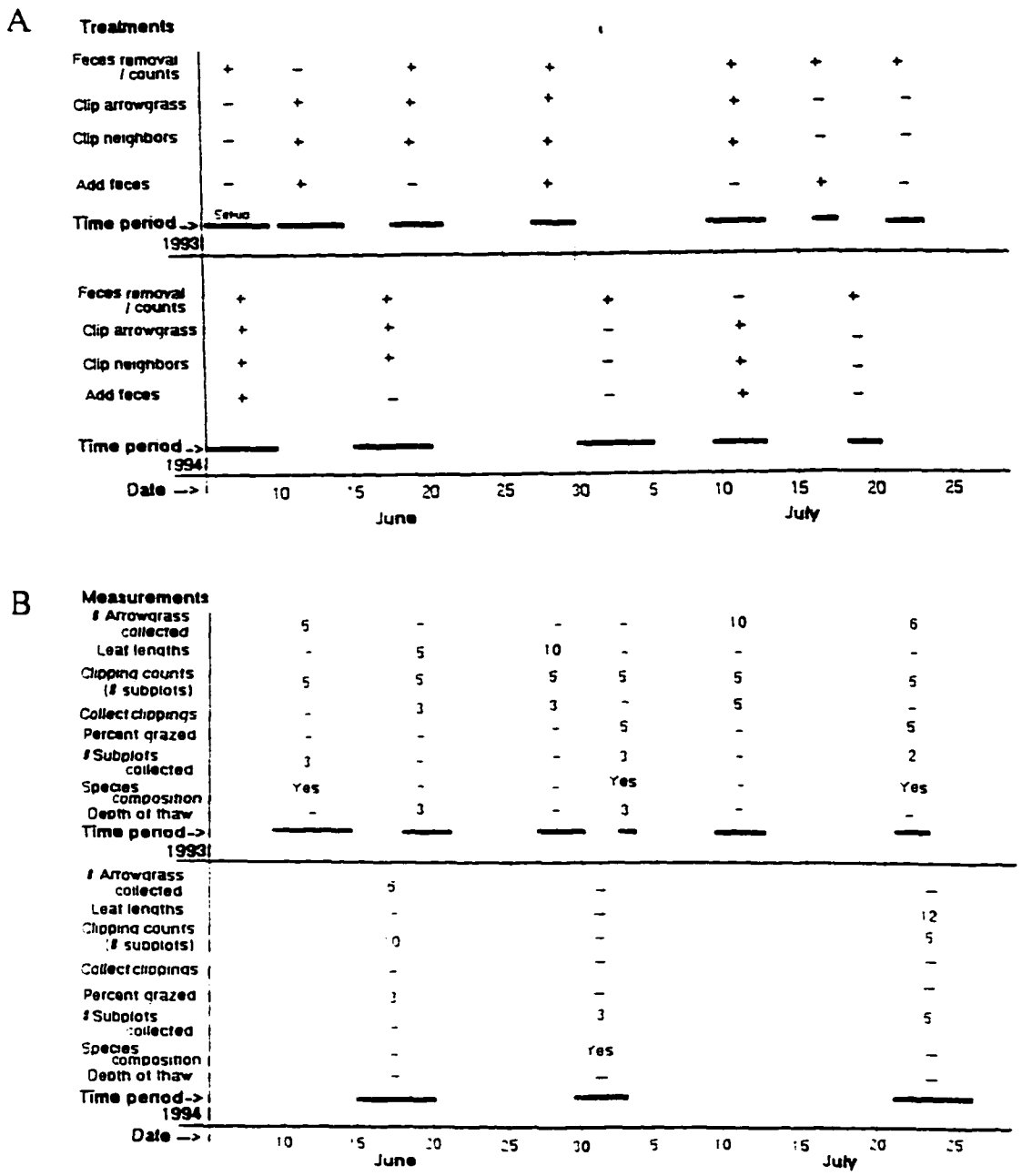

Figure 1. Details of treatments and measurements. A. Treatments on arrowgrass in 1993 and 1994 on the Yukon-Kuskokwim Delta for clipping and grazing experiments. B. Measurements on arrowgrass in 1993 and 1994 on the Yukon-Kuskokwim Delta for clipping and grazing experiment.

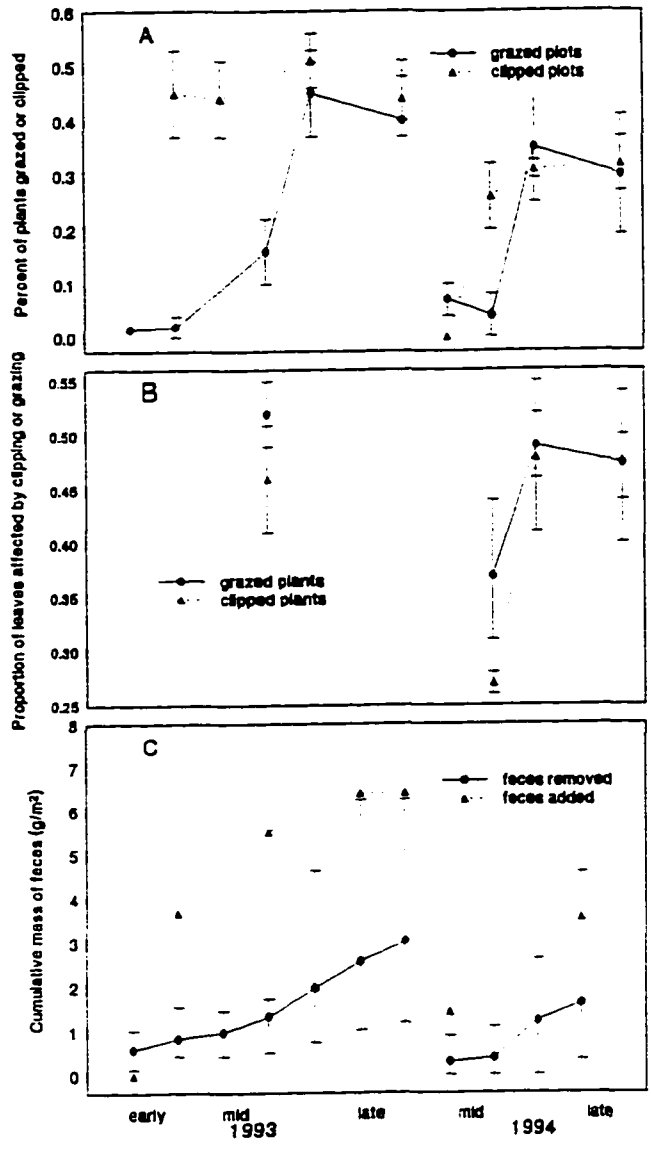

Figure 2. Comparison of clipping and grazing experimental treatments. Data are for arrowgrass on the Yukon-Kuskokwim Delta. A. Proportion of plants grazed and clipped for each time period (early June 1993, and early July and late July 1993 and 1994); error bars are standard deviations. B. Proportion of leaves grazed or clipped for each time period: error bars are standard deviations. C. Cummulative (within-year) feces mass deposited on plots at each time period. Error bars indicate ranges.

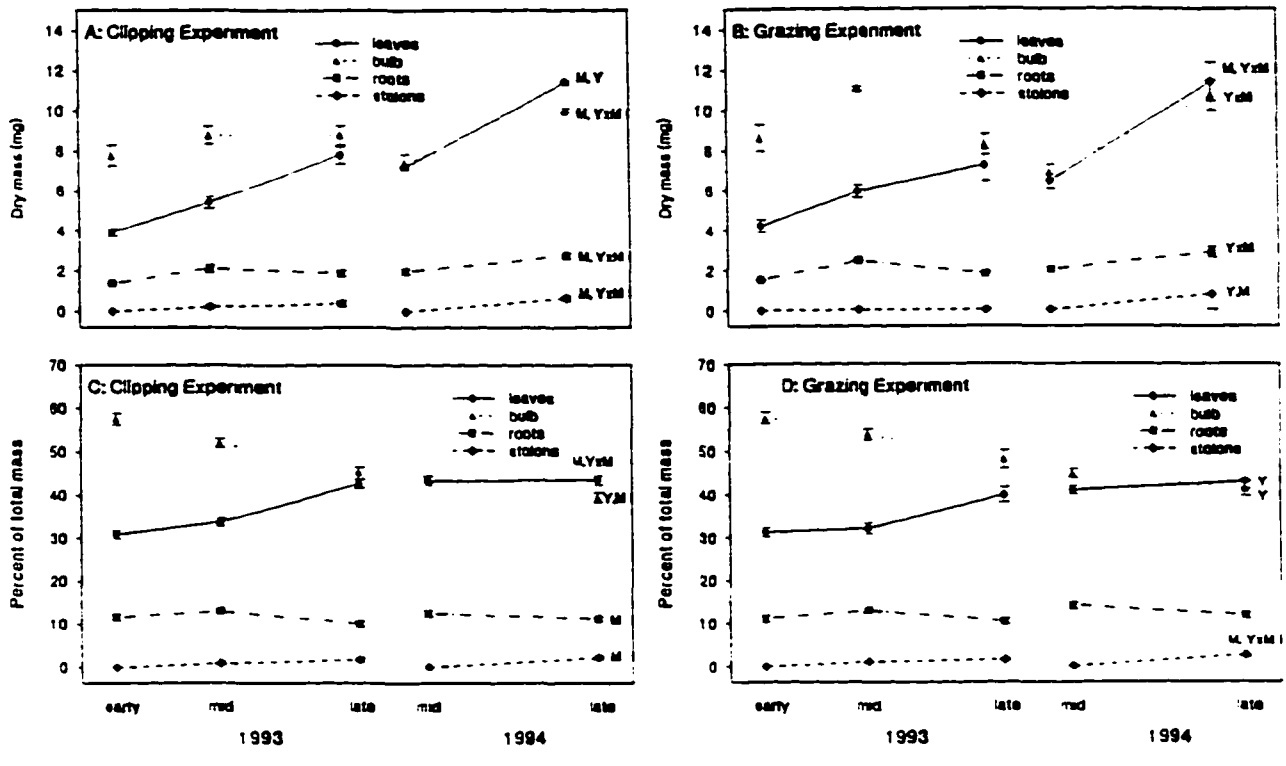

Figure 3. Change in plant mass and biomass allocation over the course of the experiment. Data are for arrowgrass on the Yukon-Kuskokwim in 1993 and 1994.Delta M (month effect), Y (year effect) and YxM (month by year interaction) refer to significant effects at $P = 0.05$ as determined by repeated measures MANOVA. All error bars indicate standard errors. A. Change in dry mass over time in the clipping experiment. B. Change in dry mass over time in the grazing experiment. C. Change in percent biomass in plant parts in the clipping experiment. D. Change in percent biomass in plant parts in the grazing experiment.

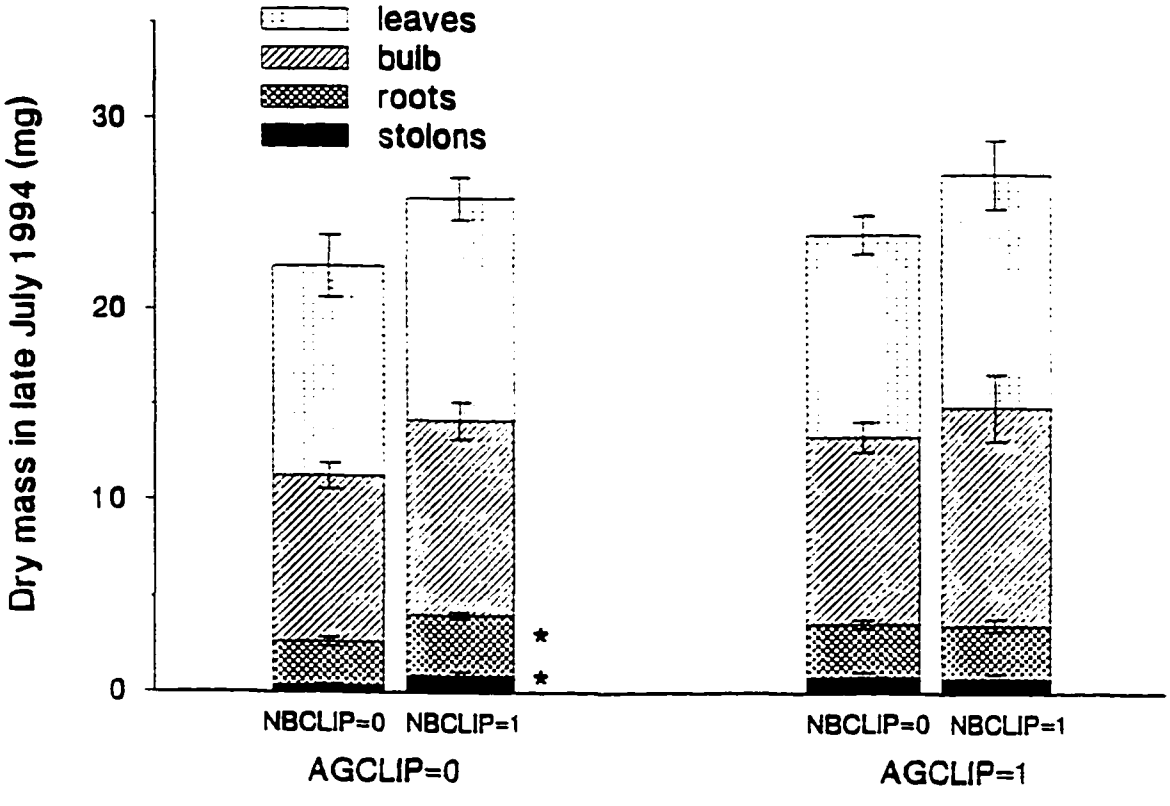

Figure 4. Interactive effects of arrowgrass clipping and neighbor clipping treatments. Data are for mass of plant parts in late July 1994 on the Yukon-Kuskokwim Delta. AGCLIP and NBCLIP refer to clipping of arrowgrass and clipping of neighbors respectively (0 = clipped, 1 = not clipped). Error bars indicate standard errors. An asterisk indicates a significant difference in mass between neighbor treatments within the arrowgrass treatment for that plant part at the $P = 0.05$ level.

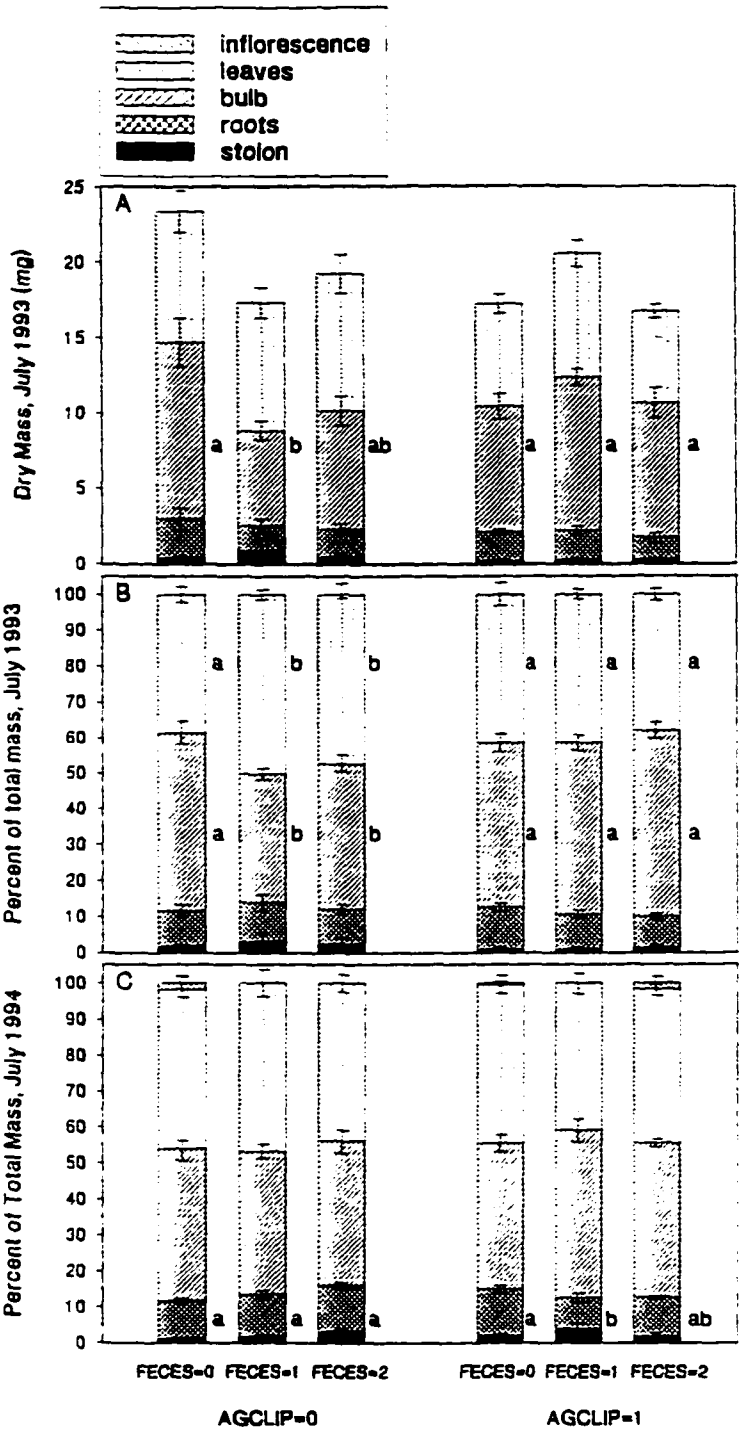

Figure 5. Interactive effects of arrowgrass clipping treatment and fertilization. Data are for mass and biomass allocation pattern for arrowgrass plant parts in 1993 and 1994 on the Yukon-Kuskokwim Delta. Error bars indicate standard errors. Different letters indicate a significant difference between fertilizer treatments within the arrowgrass treatment for that plant part at $P = 0.05$. A. Effect of arrowgrass clipping and fertilization on dry mass in late July 1993. B. Effect of arrowgrass clipping and fertilization on allocation pattern in late July 1993. C. Effect of arrowgrass clipping and fertilization on allocation pattern in late July 1994.

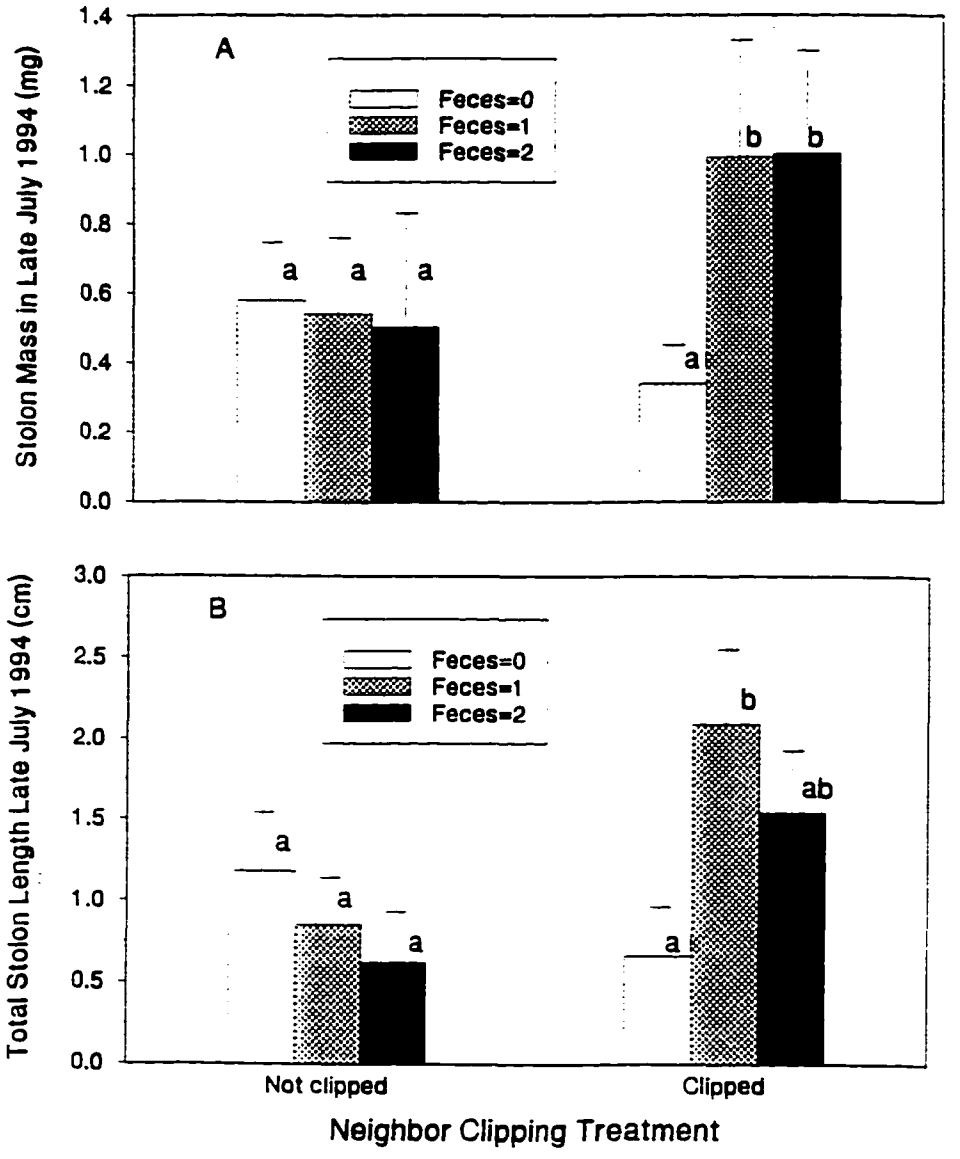

Figure 6. Interactive effects of neighbor clipping and fertilization. Data are for arrowgrass in late July 1994 on the Yukon-Kuskokwim Delta; error bars are standard errors. Different letters indicate a significant difference between fertilizer treatments within the neighbor clipping treatment at the $P = 0.05$ level. A. Effect of neighbor clipping and fertilization on mean stolon mass. B. Effect of neighbor clipping and fertilization on mean total stolon length.

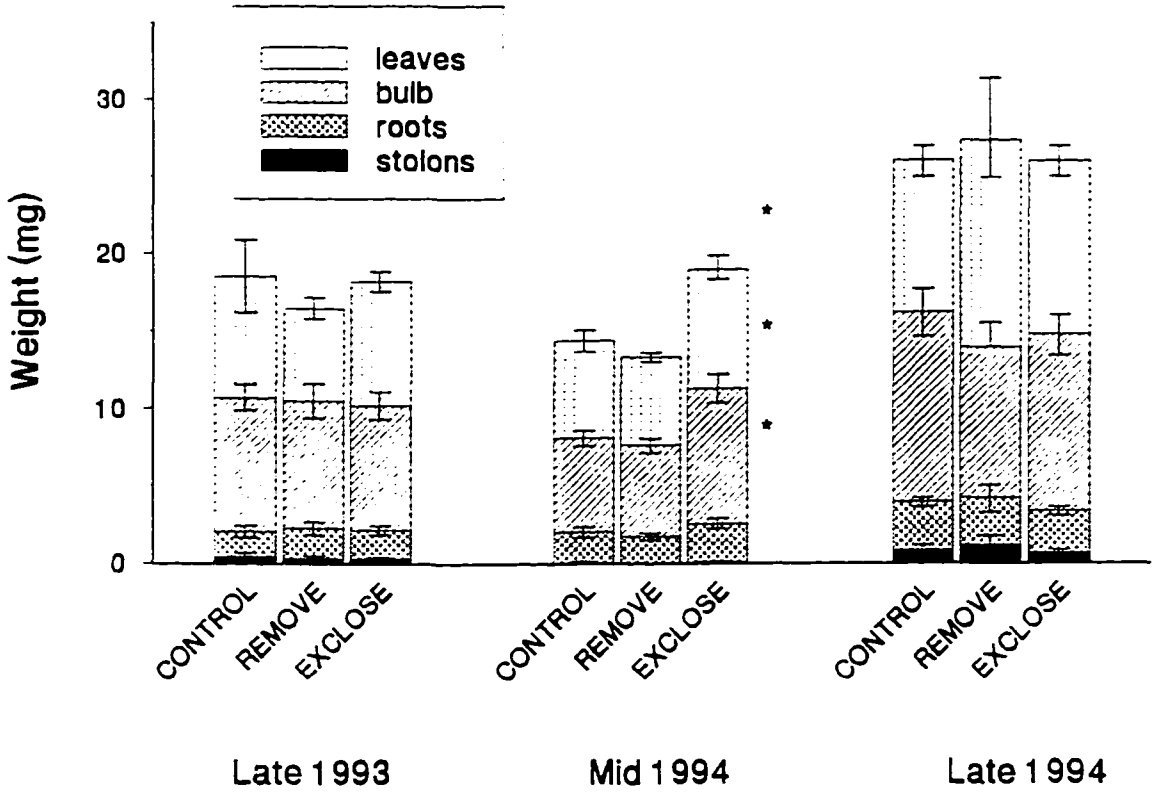

Figure 7. Effect of grazing treatments on plant mass. Data are for arrowgrass on the Yukon-Kuskokwim Delta in late July 1993, early July 1994, and late July 1994, error bars are standard errors. The asterisks indicate a significant difference (at the $P = 0.05$ level) for total mass, leaf mass and bulb mass in the EXCLOSE versus REMOVE and CONTROL treatments.

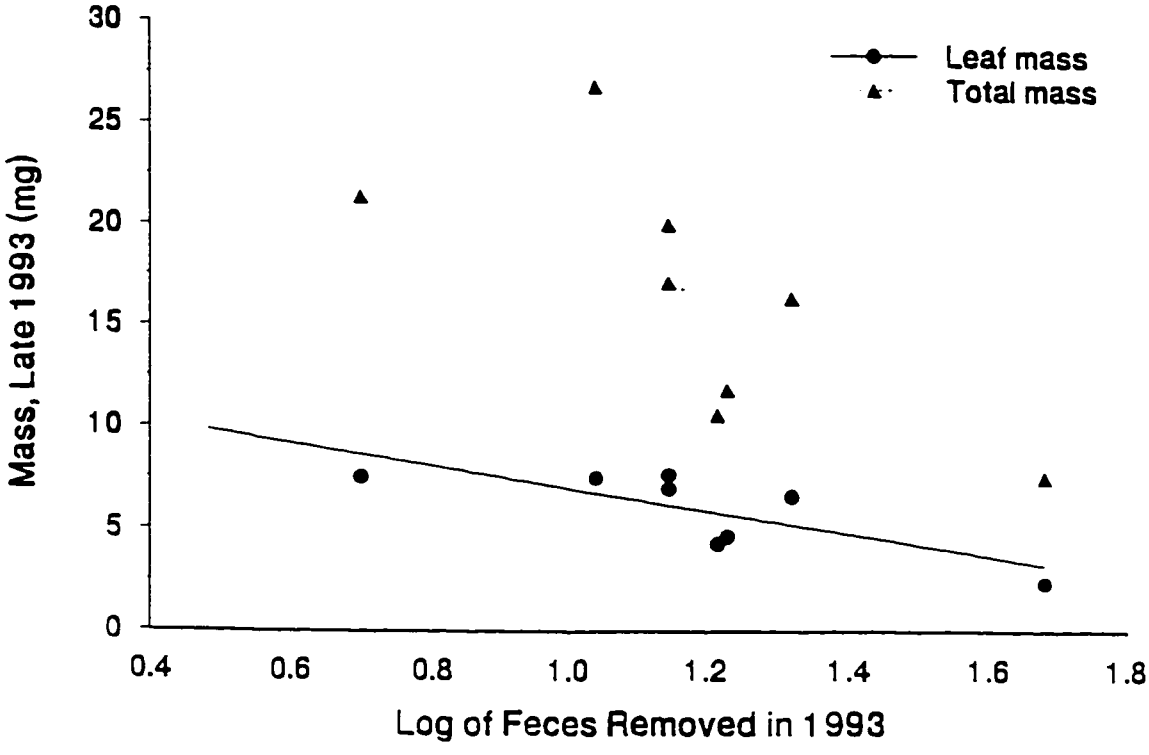

Figure 8. Relationship between grazing intensity as and total plant mass or leaf mass. Data are for arrowgrass in late July 1993 on Yukon-Kuskokwim Delta. Grazing intensity was measured by number of feces removed from REMOVE plots. For total mass, $R^2 = 0.54$, $F_{(1,6)} = 9.12$, $P = 0.023$. For leaf mass, $R^2 = 0.46$, $F_{(1,6)} = 6.90$, $P = 0.039$.

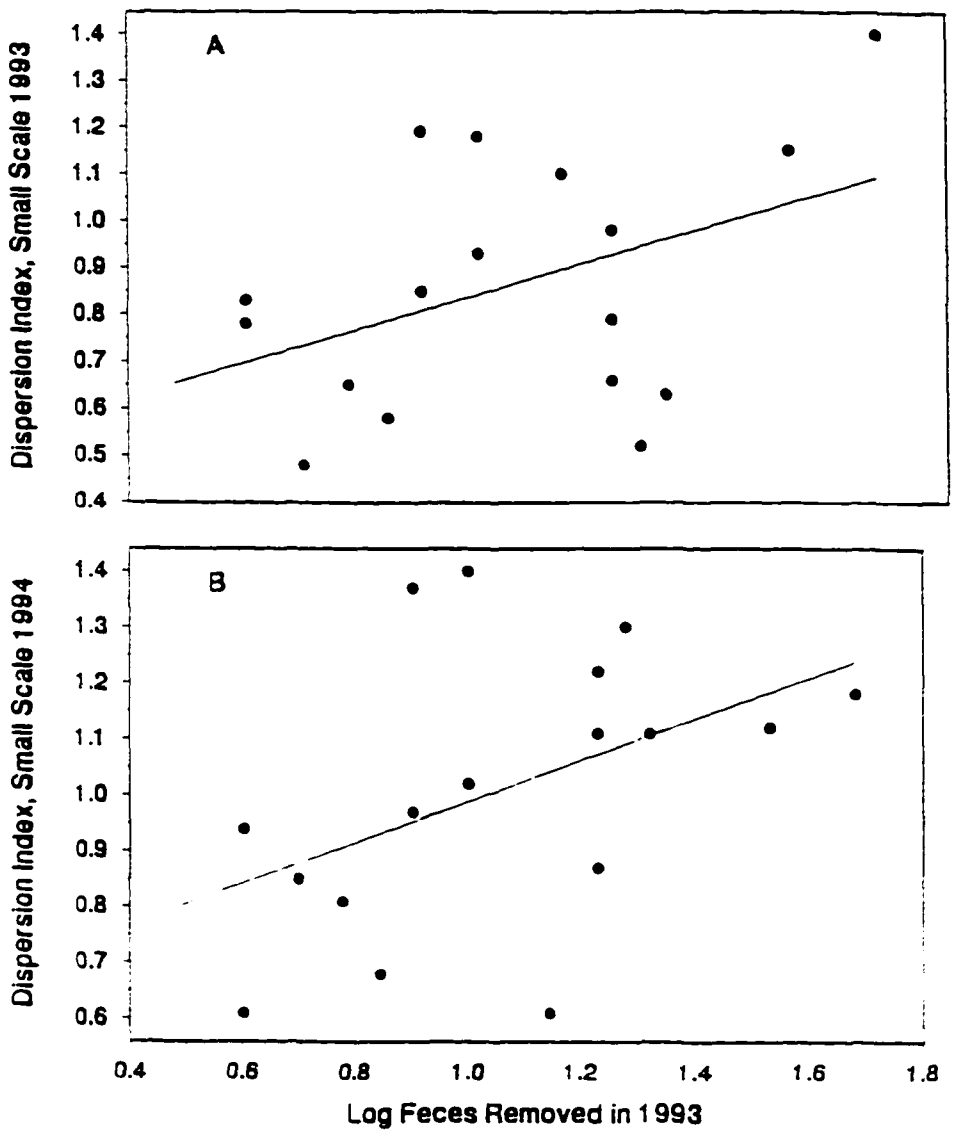

Figure 9. Relationship between grazing intensity in 1993 and dispersion index. Data are for arrowgrass at the small (25cm^2) scale on the Yukon-Kuskokwim Delta. Grazing intensity was measured as cumulative number of feces on REMOVE and CONTROL plots, and dispersion index as mean / variance for map samplings. Index>1 indicates hyperdispersion; index < 1 indicates clumping. A. Dispersion index in 1993 versus grazing intensity in 1993: R^2 = 0.12, $F_{(1,15)}$ = 3.28, P = 0.09. B. Dispersion index in 1994 versus grazing intensity in 1993: R^2 = 0.16, $F_{(1,15)}$ = 3.98, P = 0.06.

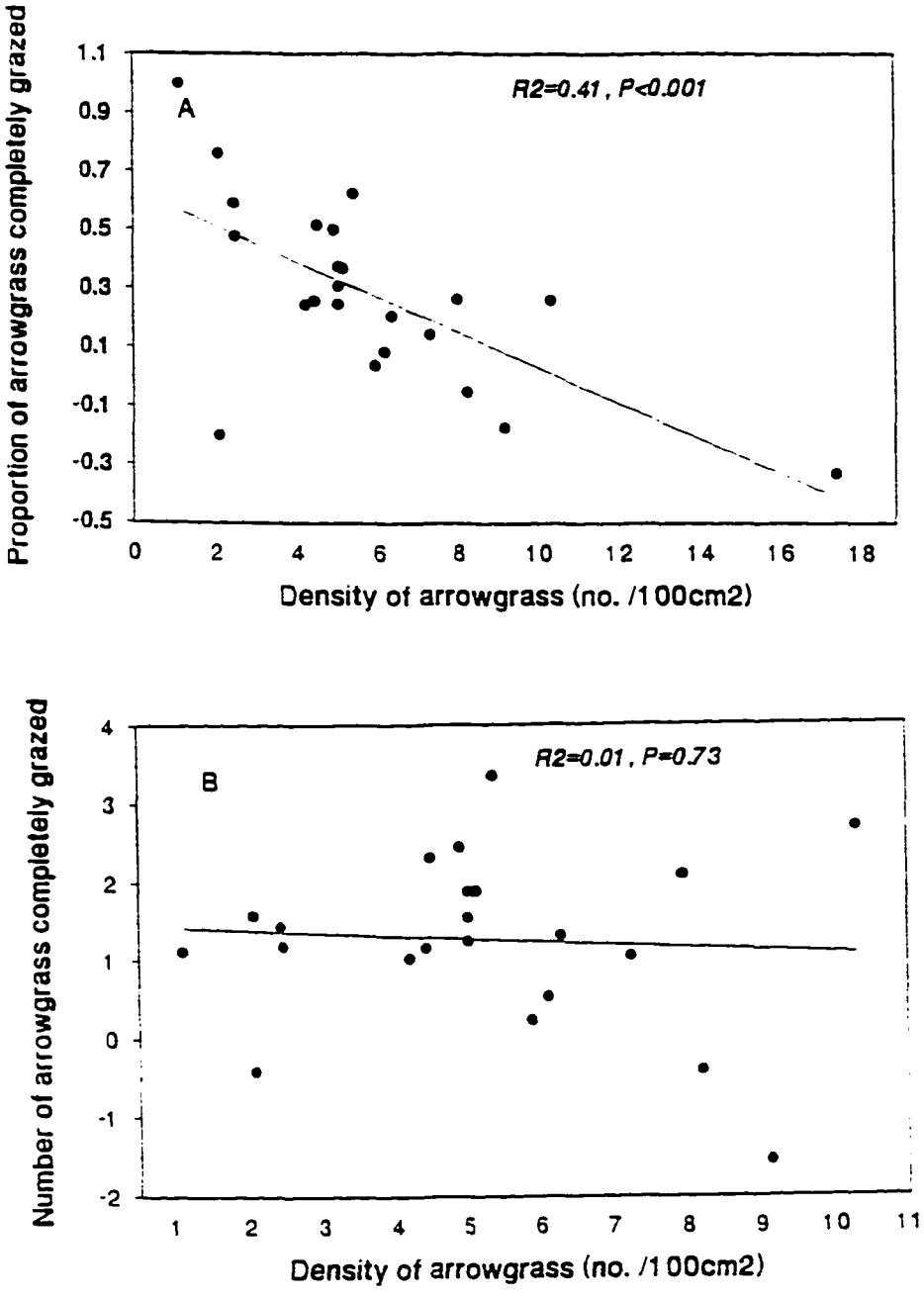

Figure 10. Relationship between arrowgrass density and proportion (A) or number (B) of plants completely grazed in the gosling experiment. The experiment was conducted in late July, 1994 on the Yukon-Kuskokwim Delta. Negative values for the proportion / number completely grazed result from cases where number of plants counted after grazing was greater than before grazing, even after the correction factor for undercounting in the field was applied.

CHAPTER FOUR:

RELATIONSHIPS BETWEEN SIZE, SURVIVAL, VEGETATIVE REPRODUCTION AND SEXUAL REPRODUCTION IN *TRIGLOCHIN PALUSTRIS* [3]

ABSTRACT

Triglochin palustris (arrowgrass) is a small herbaceous perennial that on the Yukon-Kuskokwim Delta (SW Alaska) reproduces primarily through production of stolons and bulbs, and seldom flowers. To link effects of goose herbivory on individual arrowgrass to population-level effects, we examined relationships between plant size and biomass allocation, and survival and reproduction by matching >400 individuals into groups of four and sequentially harvesting individuals from each group over the period of one year. We also examined relationships between size, vegetative reproduction, and sexual reproduction by comparing size and allocation to leaves, bulbs, roots, stolons and flowers of flowering and nonflowering plants from exclosed plots, and by comparing the effect of clipping leaves on flowering and nonflowering plants. In addition we examined four potential explanations for the low and highly variable rates of sexual reproduction: trade-offs between sexual reproduction and growth or vegetative reproduction; increased risk of herbivory for flowering individuals; the role of timing of snow melt; and costs of fertilization.

Plant size, and in particular bulb size, was positively related to probability of survival and increased reproduction, and size of the plant in the following year, but no effect of biomass allocation was detectable. A minimum size was required to produce inflorescences, but the large overlap in size between flowering and nonflowering plants suggests this alone cannot explain low rates of flowering. There was a trade-off between sexual reproduction and all other functions including vegetative reproduction. Relative investment in sexual reproduction decreased with an increase in plant size, while relative investment in vegetative reproduction was constant across all sizes.

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[3] Prepared for submission to *Oikos* as: Mulder, C.P. H., and R.W. Ruess. Relationships between size, survival, vegetative reproduction and sexual reproduction in *Triglochin palustris*.

Sexual reproduction appears to increase the risk of grazing for the flowering individual and nearby arrowgrass (which are likely related), and herbivory may be more costly for flowering plants than for nonflowering plants. Arrowgrass appears to be fully capable of self-fertilization, and evidence for the effects of snow addition or removal early in the growth season on flowering rates was inconclusive.

We conclude that in arrowgrass both intrinsic variables (e.g trade-offs between sexual reproduction and growth / vegetative reproduction) and external variables combine to create low rates of flowering, and that in particular the hypothesis that flowering results in an increase in risk of herbivory deserves further investigation.

INTRODUCTION

Herbivory usually affects the size and morphology of terrestrial plants (e.g. Mueller-Dumbois, 1972; Grant et. al, 1981; Bryant et al., 1985; Danell et al., 1985; Paige and Whitham, 1987; Doak, 1991; Mulder, 1995). In order to understand the relationship between effects of herbivory on individual plants and on population dynamics, we need to understand the effects of changes in size and biomass allocation on plant survival and reproduction. This paper addresses three aspects of this relationship for *Triglochin palustris* L. (arrowgrass; Juncaginaceae): (1) the relationship between size / biomass allocation and subsequent survival and reproduction; (2) trade-offs between sexual and vegetative reproduction; and (3) explanations for the low and variable rates of sexual reproduction.

We studied arrowgrass in subarctic saltmarsh habitat on the Yukon-Kuskokwim (Y-K) Delta in SW Alaska, where it is a preferred food for several species of geese (Sedinger and Raveling, 1984; pers. obs.) and is heavily grazed (25-55% of individuals; Chapter 3). Arrowgrass is a stoloniferous perennial that is small in this habitat (usually 3-15 cm high, < 40 mg dry weight). Its most common mode of reproduction is vegetative; during the growth season plants

produce 1-3 stolons terminating in new bulbs, which do not emerge until the following year, at which time they are no longer attached to the parent bulb (pers. obs.). Flowers are perfect and wind pollinated (Looman, 1976), but sexual reproduction is a rare occurrence (pers. obs.). Sexually reproducing plants produce a single spike-like raceme, 15-30 cm tall, with 3-7 flowers that mature into fruits containing three seeds each. Persistence of the ramet is accomplished through the production of an overwintering bulb directly above the previous bulb (pers. obs.), and plants have the potential for being long lived (15-20 years in the Canadian prairies; Looman, 1976). Arrowgrass usually emerges during the first two weeks of June (pers. obs.).

Size, Survival and Reproduction

Plant ecologists frequently use plant size or biomass as a substitute for fitness (survival and reproduction), although there is evidence that in some species, plants of intermediate size have the highest fitness (Worley and Harder, 1996). When individuals vary greatly in their allocation to various functions (e.g. leaves versus roots, or allocation to storage), interpretation of plant size becomes less clear. Arrowgrass is highly flexible in its allocation to leaves, roots and bulbs, and allocation is affected by the presence of herbivores, both directly (through biomass removal) and indirectly (through changes in fertilization and changes in competitive relationships with neighbors; Chapters 2 and 3). We tested the hypotheses that total size is correlated with survival, but that pattern of allocation (percent of biomass in leaves, roots, and bulbs) is not, by following individuals for which size and biomass allocation had been determined at the beginning of the 1994 growth season for one full year.

Probability of flowering

On the Y-K Delta arrowgrass flowers rarely, and the proportion of flowering plants varies greatly from year to year. In 1991, 1992 and 1993 we observed fewer than 10 flowering plants during the course of the summer (a flowering rate of < 0.01%), whereas in 1994 and 1995 approximately 0.06% and 0.6%, respectively, of unexclosed plants flowered. This is in contrast to other environments such as along the Tanana River in interior Alaska, where upwards of 90% of individual arrowgrass flower (*personal observation.*) When plants at our study site flower, they produce one scape with <10 flowers per plant, considerably fewer than the three scapes and 45 flowers per scape reported for Canadian prairie populations (Looman, 1976). We investigated four potential explanations for this low frequency of sexual reproduction: trade-offs between sexual reproduction and survival or vegetative reproduction; increased risk of herbivory; the role of timing of snow melt; and costs of self-fertilization.

Trade-offs between sexual and vegetative reproduction

Simple morphological constraints may dictate a minimum size before reproduction can take place (Weiner, 1988). Other hypotheses also predict the "flower at a minimum size" strategy: Loehle (1987) suggested that clonal plants should employ a "bet-hedging" strategy where a single model of reproduction should be employed only when both cannot be supported. This hypothesis suggests that size alone should predict the probability that a plant will flower, and that any large plant should engage in at least some sexual reproduction. This prediction is fairly straight-forward for plants with connected ramets, but it is less clear what should be expected in plants with

disconnected ramets (e.g. arrowgrass), which may not be able to assess total genet size. These hypotheses predict that arrowgrass flowers so rarely on the Y-K Delta because it simply seldom reaches the minimum size for flowering. A substantial overlap in size between flowering and nonflowering plants would contradict this hypothesis.

A slightly more complicated scenario results if flowering is physically possible but occurs at the expense of vegetative reproduction. Direct trade-offs between sexual and asexual reproduction have been demonstrated in some species (Sohn and Policansky 1977; Law et al., 1983; Westley, 1993; Worley and Harder, 1996), as well as between species within a genus (Sutherland and Vickery, 1988). In other species, relationships between growth and the modes of reproduction are more complicated. Hartnett (1990) reported that for four clonal composites, allocation to sexual reproduction was dependent on ramet size, while vegetative reproduction was not related to ramet or genet size. Ashmun et al. (1985) noted a positive correlation between allocation to sexual reproduction and allocation to rhizomes. While considering growth, sexual reproduction and vegetative reproduction simultaneously, Worley and Harder (1996) observed that in the adventitious bud producing species *Pinguicula vulgaris*, sexual reproduction affected vegetative reproduction and growth independently. Reekie (1991) reported negative genetic correlations between each of the modes of reproduction and growth, but not between the two types of reproduction, in a rhizomatous grass. Whether sexual reproduction always incurs a cost in terms of vegetative functions is unclear. Manipulations of reproductive effort have demonstrated costs of sexual reproduction for some species (e.g., *Polemonium foliosissimum*, Zimmerman and Pyke, 1988; *Tipularia discolor*, Snow and Whigham, 1989), or for some populations within a species (e.g., *Primula veris*, Syrjänen and Lehtilä, 1993), but other studies have shown costs only at high levels of reproduction (Antonovics, 1980), or no effect of manipulating investment on

sexual reproduction (e.g., Fox and Stevens, 1991; Jennersten, 1991). We tested for trade-offs between sexual reproduction and vegetative reproduction by examining patterns of allocation in flowering and nonflowering plants, and by manipulating reproductive investment (by removing inflorescences) and resource acquisition (by removing leaves).

Confounding effects of plant size

In many plant species, including arrowgrass (Mulder et al. 1996), size is correlated with developmental stage as well as with environmental conditions, and this leads to complications when examining only absolute allocation to sexual and vegetative reproduction (Samson and Werk, 1986; Worley and Harder, 1996) . For example, if larger plants allocate more to vegetative reproduction (regardless of flowering status), and only large plants flower, a spurious positive correlation between vegetative reproduction and sexual reproduction may occur. Similar difficulties exist when size and environment are correlated: greater proportions of flowering plants in environments with greater light availability may be the result of a direct effect of the environment (e.g., seeds germinate better and flower production is therefore of greater value) or an indirect effect of increased plant size. Several studies of perennial plants have shown that it is often size, combined with another factor (e.g. nutrient availability, light availability, decrease in growth rate) that triggers flowering (Reinartz, 1984; Lacey, 1986; Clark and Clark, 1987; Prins et al., 1990), but this outcome became apparent only when plant size was controlled. One way to eliminate the problem is to examine growth and allocation to vegetative and sexual reproduction simultaneously, but this was not possible for arrowgrass. Instead, we used analysis of covariance (ANCOVA) to compare allocation in flowering and nonflowering plants for a given plant size. Our

approach reduces confounding effects of size, but where the overlap in sizes between flowering and nonflowering plants is incomplete it does not eliminate it entirely.

One last variable that may be confounded with plant size is plant age: life-history theory predicts that organisms should invest more in reproduction as they get older and negative consequences of reproduction on future survival and reproduction decline (e.g. Gadgil and Bossert 1979; Schaffer and Gadgil, 1975; Bell, 1980). Nonetheless, clonal plants do not necessarily senesce or age physiologically, so postzygotic age may only be weakly correlated with development and reproductive success (Jackson et al., 1985), and plants may not be able to estimate age or life expectancy (Loehle, 1987). Because we were unable to estimate the age of arrowgrass individuals, any effects of size versus age were potentially confounded.

Increased risk of herbivory

A second type of explanation for low rates of flowering is that successful fruit production increases plant fitness, but that in this environment it also increases the risk of herbivory. A recent study has shown that increased risk of herbivory with increased number of flowers explains flower production in *Lathyrus vernus* (J. Ehrlén, *unpublished manuscript*). Although arrowgrass is quite cryptic (from a human viewpoint), its inflorescences are considerably taller than the leaves, and potentially more visible to geese. Hand-reared black brant (*Branta bernicla nigricans*) goslings eagerly consume inflorescences (pers. obs.) We assessed the potential for increased herbivory by comparing rates of herbivory on flowering and nonflowering plants matched on aboveground size.

Environmental factors

A third explanation for the highly variable rates of flowering concerns variation in environmental factors that do not affect plant size, but do affect the probability of sexual reproduction. In 1994, a relatively high flowering year, snow load was light and snow melt was early (B. Person, *pers. comm.*). Seed maturation in arrowgrass does not occur until the second half of August, near the end of the growing season (T. Obritskewitch, *pers. comm*), and successful seed production may only be possible in years with a relatively long growth season due to early snow melt. We tested the hypothesis that an early snow melt increases the probability of flowering by manipulating snow cover in the spring of 1995.

Costs of self-fertilization

The final explanation for low rates of sexual reproduction we investigated is that self-fertilization in arrowgrass results in low seed production. This would produce a positive feedback: where few plants flower (for other reasons), plants that do flower are unsuccessful in producing adequate numbers of seed, resulting in selection against sexual reproduction. We compared seed set in self-pollinated and open-pollinated flowers to test this hypothesis.

METHODS

Site description

This study was conducted during June, July and August 1994 and June 1995. Our study site was the Tutakoke River black brant colony, located on the Yukon-Kuskokwim Delta (Y-K Delta) in southwestern Alaska (61°15'N, 165°30' W). This area encompasses approximately 8 km^2 on both sides of the Tutakoke river. The vegetation is described in detail in Kincheloe and Stehn (1991). Arrowgrass grows on slough levees and along the edges of small ponds. This habitat

contains a mixture of species including graminoids (e.g., *Deschampsia caespitosa*, *Carex ramenskii*), herbaceous species (e.g., *Potentialla egedii*, *Stellaria humifusa*), and several species of dwarf *Salix*. The study area contains a large colony of nesting Pacific black brant and numerous cackling Canada geese (*B. canadensis minima*) (Sedinger et al., 1993); arrowgrass is a preferred forage species of both types of geese, which forage in the slough-levee habitat during the later stages of brood rearing (pers. obs.).

Experiments

We could not directly examine relationships between individuals traits at the beginning of the growth season and at later times during that year or the next because: 1) measurement of the whole plant requires excavation, which makes subsequent measurements difficult; and 2) the extremely low proportion of plants flowering would have required an enormous sample size to have reasonable power to predict flowering. A modified version of such an experiment was designed to examine the relationship between plant size, survival, and reproduction but did not provide any flowering plants. We also were limited by the low availability of flowering plants; in the process of conducting these experiments we used almost every flowering plant within several kilometers of the fieldcamp.

Tracking experiment

This experiment was designed to examine the relationship between plant size, biomass allocation, survival, and reproduction. We used matched groups of plants with sequential harvests from each group, treating each harvest as a repeated measurement on one 'individual'. Early in the growth season (early June) newly emerged arrowgrass can be transplanted without decreasing rates

of survival (Mulder et al., 1996). On 1-3 June 1994 we dug up approximately 100-110 arrowgrass from within circle of 10-m radius in each of four areas (0.5 to 2 km apart). Plants were placed into 25 groups of four or five plants visually matched to resemble each other as closely as possible in size characteristics and pattern of allocation (i.e. relative size of leaves, bulbs and roots). We measured leaves, bulb height and width, and counted number of roots > 2 mm in length for all plants. Four plants per group were returned to the ground, with matched plants placed within 10 cm of each other; all plants were returned to the same general area from which they were taken. The fifth plants (approximately 10 per area) were taken to the field laboratory and immediately dried at 60° C. On 11 July 1994, we harvested one randomly selected individual from each group, and measured and dried plants as for the first harvest On 29-30 July we carefully dug around each remaining plant and tagged any stolons we located (one or two per plant) by loosely twisting a small piece of telephone wire around it. We then left one (if none or one plant had tagged stolons) or two plants (if both had tagged stolons) in the ground, and harvested and dried (but did not measure) the remaining plants. Although plants harvested on this occasion were therefore not a random subset of available plants, our aim was to maintain the highest possible ability to examine vegetative reproduction into the following year. This may have resulted in an overestimation of rates of offspring production, but all groups were treated in the same manner so that relationships between initial size and subsequent survival and reproduction were still comparable. On 11 June 1995, we relocated as many plants as possible, and examined nearby plants for tags on old stolons. None of the parent-offspring connections was intact. Plants were harvested, separated in leaves, bulbs, roots and stolons and weighed. There were no flowering plants in any of the samples.

Plot experiment

We used plants collected in a previous set of experiments to examine differences in biomass and biomass allocation between flowering and nonflowering plants. All plants came from 1.5 m by 1.5 m plots that had been exclosed from goose grazing for two growing seasons, and that had been subjected to various levels of clipping, feces deposition, and clipping of neighbouring plants (Chapter 3, this volume). On 21-26 July 1994, we collected 12 randomly selected plants (almost all nonflowering) and five flowering plants (or as many as were available) per plot, and measured leaf lengths, plant height, inflorescence height and counted fruits on an additional 15 flowering plants per plot where available. Effects of treatments themselves on flowering and nonflowering plants are described elsewhere (Chapter 3, this volume); here we compare the two groups directly, without regard to treatment. All plants were dried at 60°C, and leaves, bulbs, roots, stolons and inflorescences were weighed separately. This experiment will be referred to as the 'plot experiment.'

Flower tracking experiment

Although the plot experiment provided a large number of ungrazed flowering plants, these plants were measured at one time only. A complementary experiment was the 'flower tracking' experiment. On 24 June 1994 we excavated 10 flowering plants and their nearest nonflowering neighbors from two areas (approx. 500 m apart). Plant height, inflorescence height, and leaf lengths were obtained on these plants. An additional 20 flowering plants and their nearest nonflowering neighbors in the same areas were tagged, and these plants were excavated on Aug. 10.

at which time seeds had ripened but not yet dispersed. All plants were dried immediately at 60° C and leaves, bulbs, roots, stolons and inflorescences were weighed separately.

Clipping experiment

In the 'clipping experiment' we manipulated leaves and flowers directly. In mid-June 1994, we located 24 flowering plants from within a 50-m radius in an area with relatively high numbers of flowering plants. Each flowering plant was matched visually with a nearby nonflowering plant of approximately the same above-ground size. At this time inflorescences on most plants had not yet emerged from between the leaves, so it is unlikely that the 'nonflowering plants' were simply flowering plants with flowers grazed off. Flowering plants were randomly allocated to one of four treatments: leaf clipping (approximately 50% of leaf biomass removed), inflorescence clipping (at the base of the inflorescence); clipping of leaves and inflorescence, or control (no clipping). Where leaves of flowering plants were clipped, the paired nonflowering plant received the same treatment, resulting in a total of six different treatments (four for flowering and two for nonflowering plants). Plants in each treatment were identifiable by the color of telephone wire with which they were tagged. The treatments allowed us to compare the relative effects of leaf removal (assumed to represent a cost) and inflorescence removal (which, if inflorescence production represents a cost, should lead to an increase in plant size), as well as the effect of inflorescence removal under more stressful conditions (leaves and flowers removed). Comparisons with nonflowering plants allowed us to examine whether removal of leaves is more costly to flowering plants than to nonflowering plants. All removed biomass was collected, dried at 60°C

and weighed. All plants were collected on 10 August, 1994, dried at 60°C, and leaves, bulbs, roots, stolons and inflorescences were weighed separately.

Bagging experiment

The 'bagging experiment' was designed to test the hypothesis that self-fertilization will result in low or no seedset. On June 29 1994, we located 33 flowering plants with pre-receptive flowers in two areas (approx. 300 m from each other) and randomly allocated them to one of two treatments: control or bagging. We initially intended to include emasculation as a third treatment, but removing the tiny anthers in the field was not feasable, and these plants became additional control plants, resulting in 22 control and 11 bagged plants. Bags consisted of a sleeve of plastic wrap put over a spiral made of telephone wire placed over the entire inflorescence and pinned to the ground with paper clips. A small space (approx. 5 mm) was left between the bottom of the sleeve and the ground for air circulation. Plants were collected on 10 August, at which stage seeds were ripe but had not yet dispersed. We scored fruits as "fully developed" or "not fully developed" (approx. one-half the size of fully developed ones), and dried and weighed all plant parts.

Snow removal experiment

The 'snow removal' experiment was designed to test the hypothesis that an early snow melt would result in a greater proportion of flowering plants. We used eighteen 1.5 m by 1.5 m plots from a previous experiment for which proportion of plants flowering in 1994 was known

(Chapter 3; these plots had not subjected to goose grazing). The plots had been exclosed for two growing seasons but not treated in any other way. Plots were randomly allocated to one of three treatments: snow removal, snow addition, or control. On 11 May 1995 the depth of the snow at three points inside and outside the plots was measured. For the snow removal treatment as much snow as possible (without damaging vegetation) was removed from inside the plots. An amount of snow similar to that removed was added to the snow addition plots. Snow depth within the plot was then remeasured at three points. On 14 June 1994 we counted the number of flowering plants in each plot and estimated the total number of plants per plot by counting all arrowgrass in three randomly located 10 cm by 10 cm quadrats.

Although sexually reproducing plants may at various points in time be in a pre-flowering, flowering or seeding stage, for simplicity we will refer to all sexually reproducing plants as "flowering plants."

Statistical analyses

All analyses were performed using SAS (v. 6.11, SAS Institute, 1996). For the tracking experiment, we used stepwise multiple regression to select variables which best explained total weight of plants in late 1994 and early 1995 (P-to-enter = 0.1, P-to-stay = 0.1). Candidate independent variables were size variables from early 1994 ("initial size"), weight and allocation variables from early 1994 and late 1994, and allocation variables from early 1995 (percent of biomass in leaves, roots, and bulbs). Separate analyses were conducted for each period. Each group of plants was treated as one individual; where more than one plant per group had been harvested at the same time, mean values for those plants were used. This violated the assumption of no variance in the independent variables, but provided a better estimate of the earlier size of the

independent variables.We used logistic stepwise regression to select the best models for probability of survival and probability of reproduction in late 1994 and early 1995, using the same candidate explanatory variables (P-to-enter = 0.1, P-to-stay = 0.05). Unlike for the size and weight variables, the status of plants at each point in time was known, so for these analyses we treated each individual plant as an independent data point.

Because in the plot experiment we collected an equal number of (primarily) nonflowering plants from each plot, but an unequal number of flowering plants (zero to five, depending on availability), we could not simply compare the means of the two groups. If, for example, in a plot with big plants there were more flowering plants, these large plants would contribute only $1/36^{th}$ of the data for nonflowering plants, but more than $1/36^{th}$ of the data for flowering plants. We therefore compared overall means of size and allocation variables using means per plot, using plot as a blocking variable. For analysis of the relationship between weight of plant parts and total plant size, however, any differences between mean plant size per plot were controlled for, and to obtain maximum power we used each plant as an independent data point. When examining the relationship between vegetative parts and flowering status, we used total nonreproductive weight (total weight minus flower and stolon weights) as a covariate. Obviously this lead to some autocorrelation, but our focus was on the difference between flowering and nonflowering plants, and we followed this by testing for differences in allocation between the two groups with total nonreproductive size as a covariate. For the plot experiment analyses, all weight data were log-transformed to improve adherence to model assumptions.

The data set for the clipping experiment was analyzed using matched pairs as blocks. All the usual weight and allocation variables were included, plus the gross weight (total weight + weight of removed tissue).

RESULTS

Tracking experiment

Matching of plants accounted for 45-81% of the variation in initial size (Table 1). In general, initial weight variables (early 1994), and particularly bulb weight or volume, significantly explained variation in subsequent survival, plant size and vegetative reproduction (Table 2). Weight variables (particularly bulb weight) in late 1994 also explained survival to early 1995 and total weight and number of offspring in early 1995 (Table 2). In contrast, initial allocation to plant parts did not explain any of the variation in later measurements. Allocations to leaves, roots and bulbs in late 1994 were negatively correlated with vegetative offspring in early 1995, indicating that stolon production came at the cost of all other plant parts. In early 1995 allocation to roots was negatively correlated with number of offspring.

Plot experiment

Mean weights per plot of all plants parts (leaves, roots, bulbs, and stolons) and total weight were significantly greater in flowering plants than in nonflowering plants (Fig. 1a). When only stolon-producing plants were included, however, no significant difference occurred between the two groups($F_{(1,11)} = 3.40, P = 0.092$). Proportion of biomass in leaves, bulbs, roots, stolons were significantly lower for flowering plants than for nonflowering plants (Fig. 1b), suggesting that allocation to sexual reproduction came at the expense of all other plant parts. Proportion of plants with stolons was marginally lower for nonflowering plants than for flowering plants (22.6% vs. 30.8%; $\chi^2_{(1)} = 3.14, P = 0.076$). Mean percent biomass in stolons for stolon-producing plants only was significantly greater for flowering plants ($F_{(1,11)} = 7.81, P = 0.017$), and

allocation to reproduction (sexual + vegetative) was significantly greater for flowering plants than for nonflowering ones ($F_{(1,28)} = 1115.72$, $P < 0.0001$). Total weight was a strong predictor of flowering (Wald $\chi^2 = 100.58$, $P < 0.0001$). Despite the large difference in size between the two groups, 57% of nonflowering plants weighed more than the smallest flowering plant.

Details of tests for interactions between flowering status and regressions of weight variables on total nonreproductive weight of plants are presented in Table 3. For leaf weight (Fig 2a) and bulb weight (Fig 2b), slopes were positive and there was a significant difference in slope for the two groups, with a steeper slope for leaf weight but a more shallow slope for bulb weight in flowering plants. For a given total nonreproductive weight, root weights for nonflowering plants were lower than for flowering plants ($F_{(1,613)} = 7.81$, $P = 0.0054$) but there was no difference in slope (Fig. 2c). The positive relationship between stolon weight and total nonreproductive weight was steeper for flowering plants than for nonflowering plants, but when only stolon-producing plants were included no difference existed between the two groups ($F_{(1,145)} = 0.05$, $P = 0.83$; Fig. 2d). In contrast, when stolon weight was regressed against total weight - stolon weight, both slope and intercept were significantly greater for nonflowering plants when all plants were included (Fig. 2e), although again there was no difference between the two groups when only plants with stolons were included (Fig. 2f). These results indicate that reproductive plants in the two groups allocate similar proportions of total biomass to vegetative reproduction, and that differences between the two groups are the result of a greater number of small plants without stolons in the nonflowering group. In contrast, total reproductive weight was significantly greater for flowering plants, whether all plants were included ($F_{(1,613)} = 787.16$, $P < 0.0001$) or only those plants with a reproductive weight greater than zero ($F_{(1,214)} = 751$, $P < 0.0001$), but the slopes for the two regression did not differ significantly.

To be able to interpret the y-intercepts, we performed linear regressions of stolon and flowering weight against total nonreproductive weight. For nonflowering plants the relationship between stolon weight and total nonreproductive weight had a slope significantly greater than zero ($t_{(514)} = 5.67$, $P < 0.0001$) but the intercept was not significantly different from zero ($t_{(514)} = 0.85$, $P = 0.39$) and the model explained little of the variation in stolon weight ($R^2 = 0.06$). This suggests a constant relative allocation to vegetative reproduction across all plant sizes (Samson and Werk, 1986). For flowering plants, the slope of the relationship between stolon weight and total nonreproductive weight was positive ($t_{(99)} = 6.74$, $P < 0.0001$) but the intercept was negative ($t_{(99)} = -3.49$, $P = 0.0007$), and the model explained considerably more of the relationship than for nonflowering plants ($R^2 = 0.32$). This suggests an increased relative allocation to vegetative reproduction with plant size. In contrast, the relationship between flower weight and total nonreproductive weight was positive ($t_{(99)} = 4.39$, $P < 0.0001$) but the intercept was positive ($t_{(99)} = 6.53$, $P < 0.0001$), suggesting a decrease in allocation to sexual reproduction with plant size. When only plants with stolons were considered, both slope and intercept were positive for stolons (nonflowering and flowering plants), and for flowers (flowering plants; $P < 0.05$).

Allocation to leaves, bulbs, roots and stolons for a given plant size was lower for flowering than for nonflowering plants ($P < 0.05$; Table 4). For nonflowering plants, as total plant weight increased there was an increase in allocation to leaves and stolons, a decrease in allocation to roots, and no change in allocation to bulbs (Fig. 3). In contrast, for nonflowering plants an increase in total plant weight resulted in no significant changes in allocation to roots, leaves, or bulbs, an increase in allocation to stolons, and a decrease in allocation to flowers, (Fig. 3) resulting in no change in total allocation to reproduction with plant weight. When only plants producing

stolons were included, there was no relationship between total plant size and allocation to stolons for either group (Fig. 3e).

For flowering plants, there was no relationship between percent weight in stolons and percent weight in flowers $tT_{(99)} = -1.68$, $P = 0.095$), and flower weight did not explain stolon weight after correcting for plant size ($t_{(99)} = 0.57$, $P = 0.57$).

Flower tracking experiment

All plants except one (a flowering plant) were grazed in this experiment, but in seven of 17 flowering plants at least some fruits remained on the plant. Initial plant height, total leaf length, and number of leaves (the characteristics on which the plants were matched) were not different between flowering and nonflowering plants ($P > 0.1$ for all). Despite this lack of difference, initial leaf weight was significantly greater for flowering plants ($F_{(1,18)} = 6.66$, $P = 0.0018$), as were initial bulb height ($F_{(1,18)} = 11.24$), width ($F_{(1,18)} = 1.24$, $P = 0.0026$), and weight ($F_{(1,18)} = 6.66$, $P = 0.0018$), reproductive weight ($F_{(1,18)} = 56.37$, $P < 0.0001$) and total weight ($F_{(1,18)} = 21.35$, $P = 0.0002$; Fig. 4a). Of the allocation variables, percent biomass in roots was lower ($F_{(1,18)} = 4.64$, $P = 0.045$) and percent biomass in reproductive tissues was higher ($F_{(1,18)} = 22.0$, $P = 0.0002$) in flowering plants, suggesting that flower production was primarily at the cost of roots. However, when analyzed with total nonreproductive weight as a covariate, there were no significant differences between flowering and nonflowering plants.

Late in the season (August 10) flowering plants had significantly greater leaves ($F_{(1,30)} = 4.36$, $P = 0.045$) and marginally greater bulbs ($F_{(1,28)} = 3.66$, $P = 0.066$), but of the allocation variables only root percent biomass was significantly lower in flowering plants($F_{(1,28)} = 4.96$, $P =$

0.034). When total nonreproductive weight was added as a covariate, however, the only significant difference between the two groups was in stolon weight (Fig. 4b). The slopes of the two lines for stolon weight against total nonreproductive weight were significantly different ($F_{(1,26)} = 13.54$, $P = 0.0011$), with a significant positive relationship for nonflowering plants ($t_{(13)} = 3.90$, $P = 0.0018$) but no relationship for flowering plants ($t_{(13)} = 0.61$, $P = 0.55$). In contrast, there was a significant positive relationship for flowering plants between flower weight and vegetative weight (total weight - flower weight; $t_{(13)} = 2.68$, $P = 0.018$) The data provided no evidence for a trade-off between sexual and vegetative reproduction after correcting for total weight ($t_{(13)} = -1.24$, $P = 0.24$).

Clipping experiment

There were no significant differences in initial plant height, number of leaves, or total leaf lengths between treatments ($P > 0.1$). Mean leaf mass removed was not different for flowering versus nonflowering plants ($P > 0.1$), but flower biomass removed from flowering plants was significantly less than leaf biomass removed (1.5± 0.2mg vs. 3.4± 0.4 mg; $F_{(1,41)} = 8.70$, $P = 0.0052$).

Herbivory affected a significantly greater proportion of plants with intact inflorescences (50.0%) than without intact inflorescences (6.3%; $\chi^2_{(1)} = 6.2$, $P < 0.025$). For nonflowering plants, clipping leaves had no effect on weight of any plant part (Fig.5a) or on allocation pattern (Fig. 5b). Clipping did appear to have an effect on flowering plants (Fig. 5a), but differences were not significant ($P > 0.1$ for all plant parts). Unclipped flowering plants had a significantly greater leaf weight ($F_{(1,17)} = 8.90$, $P = 0.0083$), root weight ($F_{(1,14)} = 5.10$, $P = 0.040$), bulb weight ($F_{(1,14)} = 5.23$, $P = 0.038$), reproductive weight ($F_{(1,13)} = 9.32$, $P = 0.009$) and total weight ($F_{(1,3)} = 13.23$, $P = 0.003$), and lower percent biomass in leaves ($F_{(1,13)} = 7.38$, $P = 0.0176$) than did unclipped

nonflowering plants. However, none of these variables differed between flowering plants with clipped leaves and nonflowering plants with clipped leaves (leaf weight: $F_{(1,17)} = 2.99$, $P = 0.102$; root weight: $F_{(1,14)} = 0.83$, $P = 0.38$; bulb weight: $F_{(1,14)} = 3.78$, $P = 0.072$; reproductive weight: $F_{(1,13)} = 0.43$, $P = 0.52$; total weight: $F_{(1,13)} = 3.87$, $P = 0.071$; percent leaf biomass: $F_{(1,13)} = 2.33$, $P = 0.15$), although nonflowering plants with leaves clipped had marginally greater stolon weights than flowering plants with clipped leaves ($F_{(1,13)} = 4.32$, $P = 0.058$). No significant differences occurred between flowering plants with leaves removed and flowering plants with flowers removed ($P > 0.1$ for all variables). Flowering plants with only flowers clipped had a greater proportion of biomass in leaves than plants with flowers and leaves clipped ($F_{(1,13)} = 4.66$, $P = 0.050$), but there were no other significant differences between the two groups ($P > 0.1$ for all). There were no significant differences in proportion of plants producing stolons between flowering and nonflowering plants or clipped and non-clipped plants ($P > 0.1$ for all).

Bagging experiment

When all plants were compared, bagged plants had a significantly greater leaf weight (23.03 ±1.4 mg vs. 15.84 ±1.2 mg; $F_{(1,30)} = 14.1$, $P = 0.0007$), inflorescence weight (18.05±2.2 mg vs. 15.84±1.2 mg; $F_{(1,29)} = 7.38$, $P = 0.011$), and fruit number (5.17±0.3 vs. 3.36±0.3; $F_{(1,24)} = 17.58$, $P = 0.0003$). However, none of the 12 bagged plants had been grazed, while of 23 unbagged plants nine were known to be grazed, and for eight the grazing status was unknown ($\chi^2_{(1)} = 9.50$, $P = 0.002$ for known status plants only). When we reran the comparisons including only plants known to be ungrazed, only leaf weight was significantly different (unbagged: 15.58±1.6 mg: bagged: 23.03±1.4 mg: $F_{(1,16)} = 10.03$, $P = 0.006$). Values for inflorescence weight and fruit number were higher (although not significantly so) for bagged plants, so arrowgrass appeared to be

self-fertile. There was some evidence, however, that fruits in bagged plants did not develop normally. Fruits did not develop to full size in only one of the unbagged plants, while in three bagged plants fruits failed to develop. This difference was not significant ($\chi^2_{(1)} = 1.78$, $P = 0.18$) but had low power. None of the other variables were significantly different ($P > 0.10$).

Snow removal experiment

Snow manipulation resulted in a snowdepth of 6.4±5cm in plots with snow removed, 8.0. ±2 cm in control plots, and 16.3±4 cm in snow addition plots. Plots with snow removed had the most flowers per plot (Fig. 6a), the highest proportion of plants flowering (Fig. 6b), and the highest ratio of plants flowering in 1995 to plants flowering in 1994. No significant differences occurred between treatments in number of flowers, proportion of plants flowering, or ratio of 1995 to 1994 flowering plants ($P > 0.1$). There was no relationship between number of flowers and snow depth before treatment ($t_{(16)} = 0.43$, $P = 0.67$)or after treatment ($t_{(16)} = -1.24$, $P = .23$).

DISCUSSION

Relationships between plant size, allocation, and fitness.

In arrowgrass, survival and reproduction are positively related to plant size, but unrelated to biomass allocation. Probability of survival was greater for plants with a large initial leaf number and bulb volume, and large total weight in late 1994, while plant size in the following year was positively correlated with initial total size. The most important predictor of offspring production in the following year was bulb volume. The data provided no evidence that allocation pattern had any effect on size, survival or reproduction in the following year. Geese affect both

plant size and biomass allocation (Chapter 3); our results suggest that only changes in plant size will have consequences for population dynamics of arrowgrass.

Trade-offs between size, sexual reproduction, and vegetative reproduction

Results from both the plot and the flower tracking experiments show that small plants do not flower and that flowering plants are larger than nonflowering plants in every respect, suggesting a minimum size requirement for flowering in arrowgrass. Nonetheless, 57% of nonflowering plants were larger than the smallest flowering plant. A minimum size requirement can therefore explain why some small plants do not flower, but not why so few larger ones do.

In the plot experiment, allocation to flowering was primarily at the expense of bulbs: bulbs in flowering plants were smaller than for nonflowering plants of the same size (even when reproductive tissues were not included in size), and the difference between the groups grew with increasing plant size. In contrast, roots of flowering plants consistently weighed more than for nonflowering plants of the same size, whereas leaf weight was lower for small plants but greater for large plants. There is clearly a trade-off between sexual reproduction and vegetative reproduction: for a particular total weight, flowering plants allocated less to stolons than did nonflowering plants. Data from the flower track experiment, which showed an increase in stolon weight with total weight for nonflowering plants, but not for flowering plants, also suggest a trade-off. In the plot experiment, however, allocation to stolons relative to nonreproductive size did not differ between the two groups, suggesting that the trade-off is between sexual reproduction on the one hand, and vegetative growth and reproduction on the other hand, rather than between the two modes of reproduction *per se*. This is supported by the lack of a direct negative relationship

between the two modes of reproduction after correction for plant size. The relationship between reproduction and total size differed between the two modes of reproduction: allocation to stolons (for plants producing stolons) was constant across all plant sizes, while allocation to inflorescences dropped with plant size. In other words, although absolute investment increases with plant size for both modes of reproduction, relative investment drops for sexual reproduction. Such a relationship between sexual reproduction and size has been reported in many species of annual and perennial herbaceous plants (Solbrig, 1981; Aker, 1982; Samson and Werk, 1986), although our study contradicts the prediction of Samson and Werk (1986) that no relationship between sexual reproduction and plant size may be expected when vegetative reproduction also is present. Thus the apparent substantial investment in sexual reproduction limits both bulb development and vegetative reproduction. This outcome may help explain why small plants, even though they possess the minimal required resources, often do not flower. The decrease in relative cost of sexual reproduction with plant size also may explain why larger plants do flower.

In the flower clipping experiment, removing inflorescences at an early stage had an effect similar to that of removing leaves, and there was no evidence that release from investment in sexual reproduction resulted in increased growth. Whereas unclipped flowering plants were significantly larger than unclipped nonflowering plants, no difference existed between clipped flowering plants and clipped nonflowering plants, suggesting that flowering plants are more affected by clipping of leaves than nonflowering plants. Under the clipped conditions nonflowering plants also had larger stolons than flowering plants. This suggests that stress induced by herbivory may account for the lack of a positive relationship between stolon weight and total weight for flowering plants in the flower tracking experiment. The removal of inflorescences (or parts of inflorescences) of unclipped plants by geese may have reduced the difference between plants from which we removed

inflorescences and those which were not treated, but herbivory probably took place after flowering was completed so that the cost of producing an inflorescence in plants which were grazed is unlikely to have been completely eliminated.

Several hypotheses have been put forward to explain the lack of a cost of sexual reproduction in some species. Many long-lived perennials may reproduce at a continuously low level, with minor effects on growth and survival (Schaffer, 1974; Stearns, 1976). This is unlikely to hold for arrowgrass, which rarely flowers and for which inflorescences represent 25-60% of total weight. Tuomi et al. (1983) suggested that reproducing individuals can change their resource intake and thus compensate for the additional costs, whereas others have postulated that trade-offs between sexual and vegetative functions may exist in some environments but not in others (Stearns, 1989; Syrjänen and Lehtilä, 1993). These hypotheses do not suggest that costs of reproduction are nonexistent, but rather that costs will be observable only when they are extreme. If flowering arrowgrass are present only in relatively resource-rich microhabitats, and this is expressed in characteristics other than size (e.g. higher nitrogen concentrations), such costs may be difficult to detect.

Flowering and the risk of herbivory

Almost every plant (flowering or nonflowering) in the flower tracking experiment was grazed, so this experiment did not demonstrate that flowering increases the probability of being grazed. In the clipping experiment, however, plants with intact inflorescences were more likely to be grazed than other plants, and the rates of herbivory in these experiments were much higher than those experienced by other unexclosed plants (25-50% over the course of 2 months). This strongly suggests that the presence of flowering plants may act as an attractant to geese, and result in

grazing of not just the flowering plants but nonflowering neighboring arrowgrass also. Stolons are usually < 15 cm long (pers. obs) and neighbors are likely to be closely related. Thus flowering may entail a double risk if it increases not only herbivory of the individual but also of relatives. Data from this study indicate that this hypothesis merits further attention.

Flowering and snow load

The results of the snow removal experiment did not provide strong support for the hypothesis that flowering is more likely in year in which snow melts early: although plots with snow removed had the most flowering plants and the highest ratio of plants flowering in 1995 compared with the previous years, these differences were not statistically significant. Given the great variability among plots and the low proportions of flowering plants, however, overall power in this test was low. This hypothesis deserves more attention, particularly in explaining the high spatial and temporal variability in proportion of plants flowering.

Costs of self-fertilization

The hypothesis that arrowgrass does not flower when flowering rates are low because it cannot self-fertilize was not supported. Plants were clearly self-compatible, with no differences in fruit numbers between self-pollinated and open-pollinated flowers. Although there may be a cost involved at a later stage (as suggested by the slight increase in number of underdeveloped fruits in bagged plants), evidence from this experiment does not support the hypothesis that lack of self-compatibility could have resulted in a negative -eedback mechanism in an environment with low rates of flowering due to other causes.

Conclusions

The relationship between plant size or biomass allocation and future survival and reproduction turned out to be fairly simple: size matters, allocation (at least at the beginning of the growth season) does not. This study did not provide a simple explanation for why arrowgrass flowers so rarely on the Y-K Delta, but both intrinsic explanations (costs of sexual reproduction to the plants) and external explanations appear to play a role. A minimum size appears to be required to produce inflorescences, there is a trade-off between sexual reproduction and all other functions including vegetative reproduction, and relative cost of sexual reproduction decreases with increased plant size while relative cost of vegetative reproduction is constant. In addition, in arrowgrass flowering appears to increase the risk of being grazed of the flowering individual and nearby arrowgrass (which are likely to be related to the flowering individual), and herbivory may be more costly for flowering plants than for nonflowering plants. We believe that the potential for increased risk of herbivory deserves more attention, in this system as well as others. Finally, small-scale resource availability which does not affect only plant size may play a role, and in this extreme environment the role of annual variation in weather cannot be ruled out.

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Table 1. Effectiveness of matching in the tracking experiment. Data are for arrowgrass on the Yukon-Kuskokwim Delta as measured by proportion of variation in initial measurements explained by matching in groups in early June 1994. SS refers to the sums of squares for each variable.

Variable	SS explained by group match	Unexplained SS	Model R^2
Plant height	619.5	288.1	68.3
Leaf number	98.0	62.0	45.4
Total leaf length	9070.7	2141.1	80.9
Bulb height	11.3	5.5	67.2
Bulb width	1.3	0.8	64.5
Bulb volume	3.6	1.5	70.3
Root number	638.5	785.1	44.9

Table 2. Tracking experiment: models of best fit using stepwise regression (total weight and number of offspring, F values) or logistic stepwise regression (probability of survival and reproduction, Wald χ^2 values). Data are for arrowgrass on the Yukon-Kuskokwim Delta in 1994 and 1995. Significance level to enter = 0.1, significance level to exit = 0.05 for logistic regression, 0.1 for linear regressions. Separate models were run for independent variables from different time periods.

Dependent variable	Independent variable	Direction	F or χ^2 (df)	P
Survival until collection	Initial leaf number	positive	7.10 (230)	0.008
Survival until 1995	Initial bulb volume	positive	5.32 (43)	0.021
Survival from late 1994 to 1995	Total weight late 1994	positive	4.94 (43)	0.026
Total weight late 1994	Initial root number	positive	4.05 (1,34)	0.052
	Initial bulb volume	positive	3.03 (1,34)	0.091
Total weight early 1995	Initial total weight	positive	3.07 (1,22)	.094
Reproduction late 1994	Initial leaf weight	positive	13.59 (180)	0.0002
	Initial bulb weight	positive	3.48 (180)	0.004
	Leaf weight late 1994	positive	26.45 (180)	<.0001
Offspring in early 1995	Initial bulb volume	positive	7.15 (1,22)	0.014
	Stolon weight late 1994	positive	27.30 (1,22)	<.0001

Table 3. Plot experiment: Interactions between flowering status and regressions of weight variables on total nonreproductive weight or on total weight minus stolon weight. Data are for arrowgrass on the Yukon-Kuskokwim Delta in late July 1994. All regressions have positive slopes.

Dependent variable	Difference in slope	*F*(df)	*P*
Independent variable: total nonreproductive weight			
Leaf weight	steeper for flowering plants	6.56 (1,612)	0.011
Bulb weight	steeper for nonflowering plants	7.34 (1,612)	0.007
Root weight	no significant difference	0.11 (1,612)	0.74
Stolon weight (all plants)	steeper for flowering plants	18.08 (1,162)	<0.0001
Stolon weight (plants with stolons only)	no significant difference	0.05 (1,144)	0.830
Total reproductive weight (all plants)	no significant difference	2.44 (1,612)	0.119
Total reproductive weight (reproductive plants only)	no significant difference	0.01 (1,214)	0.92
Independent variable: total weight minus stolon weight:			
Stolon weight (all plants)	steeper for nonflowering plants	25.75 (1,612)	<0.0001
Stolon weight (plants with stolons only)	no significant difference	0.53 (1,144)	<.0001

Table 4. Plot experiment: Relationships between allocation variables and total weight for flowering and nonflowering plants. Data are for arrowgrass on the Yukon-Kuskokwim Delta in 1994. A '*' indicates a significant difference between slopes for the two groups ($P < 0.05$).

Dependent variable	Nonflowering Plants			Flowering Plants		
	Direction	*T* (df)	*P*	Direction	*T* (df)	*P*
% Biomass in leaves*	no relationship	1.75	0.081	positive	3.10	0.0025
% Biomass in roots	negative	-5.09	<0.0001	no relationship	-1.04	0.30
% Biomass in bulbs	no relationship	-0.49	0.62	no relationship	-1.79	0.08
% Biomass in stolons (all plants)	positive	5.54	<0.0001	positive	6.34	<0.0001
% Biomass in stolons (plants with stolons)	no relationship	1.80	0.18	no relationship	0.08	0.79
% Biomass in flowers	____			negative	-2.30	0.023
% Biomass in reproduction	positive	5.54	<0.001	no relationship	-1.29	0.199

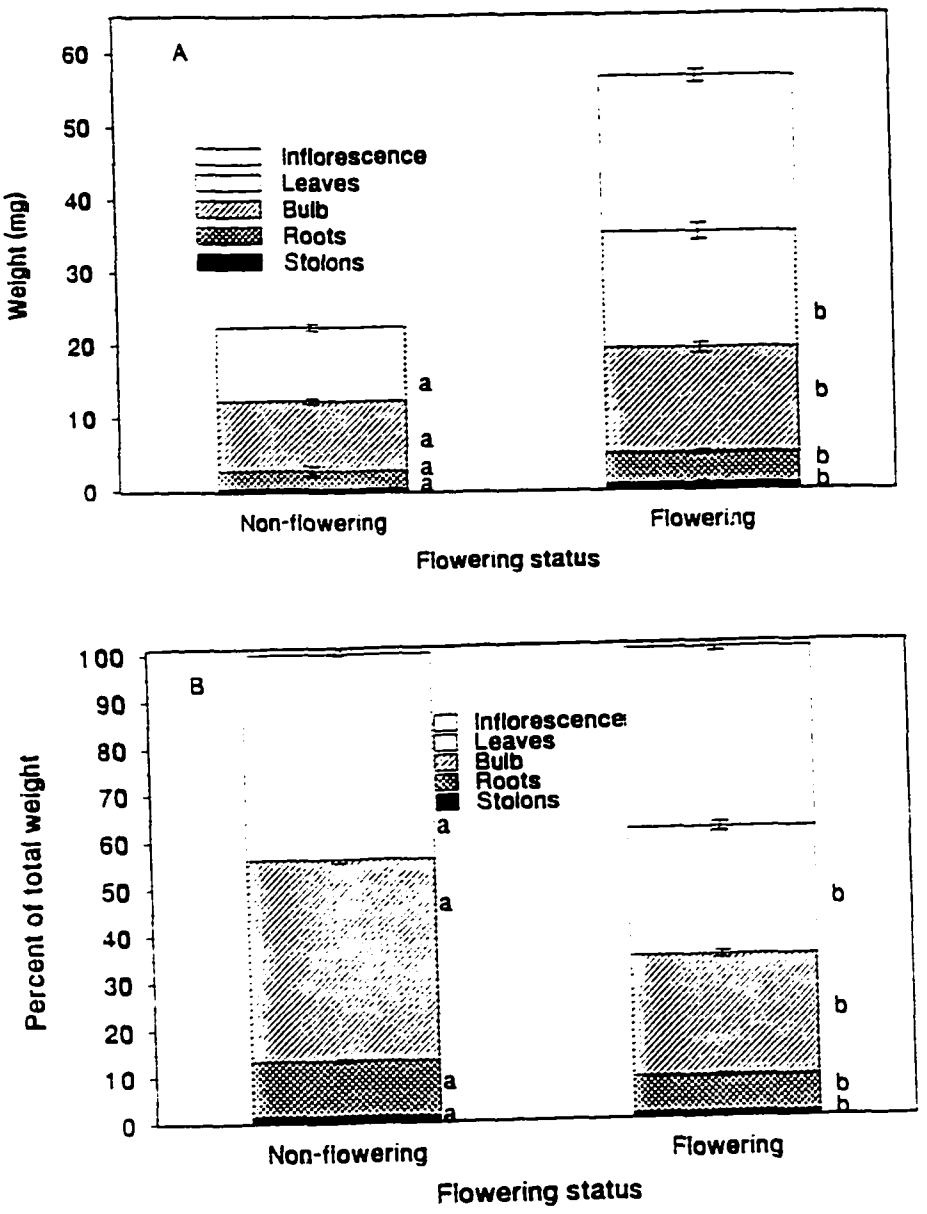


Figure 1. Plot experiment results: flowering versus nonflowering plants. Data are for arrowgrass on the Yukon-Kuskokwim Delta in late July, 1994. a) Weight of flowering and nonflowering plants; b) Proportion of weight for each plant part for flowering and nonflowering plants. Different letters signify a significant difference between flowering and nonflowering plant at the $P = 0.05$ level. Error bars are standard errors (using each plant as an independent data point).

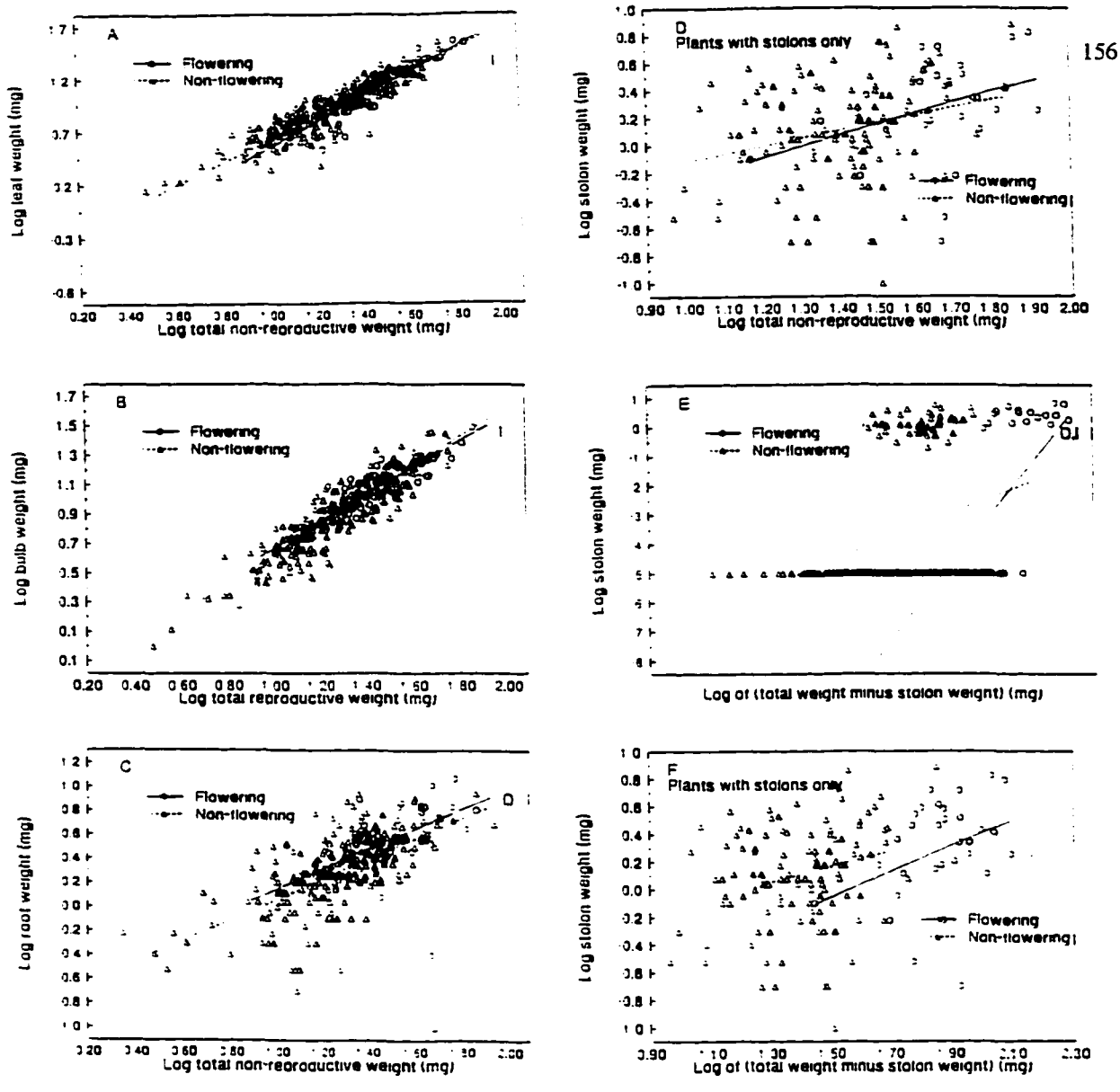


Figure 2. Plot experiment results: weights of flowering and nonflowering plants corrected for total nonreproductive weight. A 'D' indicates a significant difference in intercepts between the two groups, but not in slope; an 'I' indicates a significant interaction between flowering status and total nonreproductive weight. Data are for late July 1994. For clarity, in most figures only every other datapoint is pictured. a). Log of leaf weight versus total nonreproductive weight. b). Log of bulb weight versus log of total nonreproductive weight. c). Log of root weight versus total nonreproductive weight. d). Log of stolon weight versus total nonreproductive weight for plants which produced stolons only (all datapoints pictured). e). Log of stolon weight versus log of total weight minus stolon weight for all plants . f). Log of total weight minus stolon weight for plants which produced stolons only (all datapoints pictured).

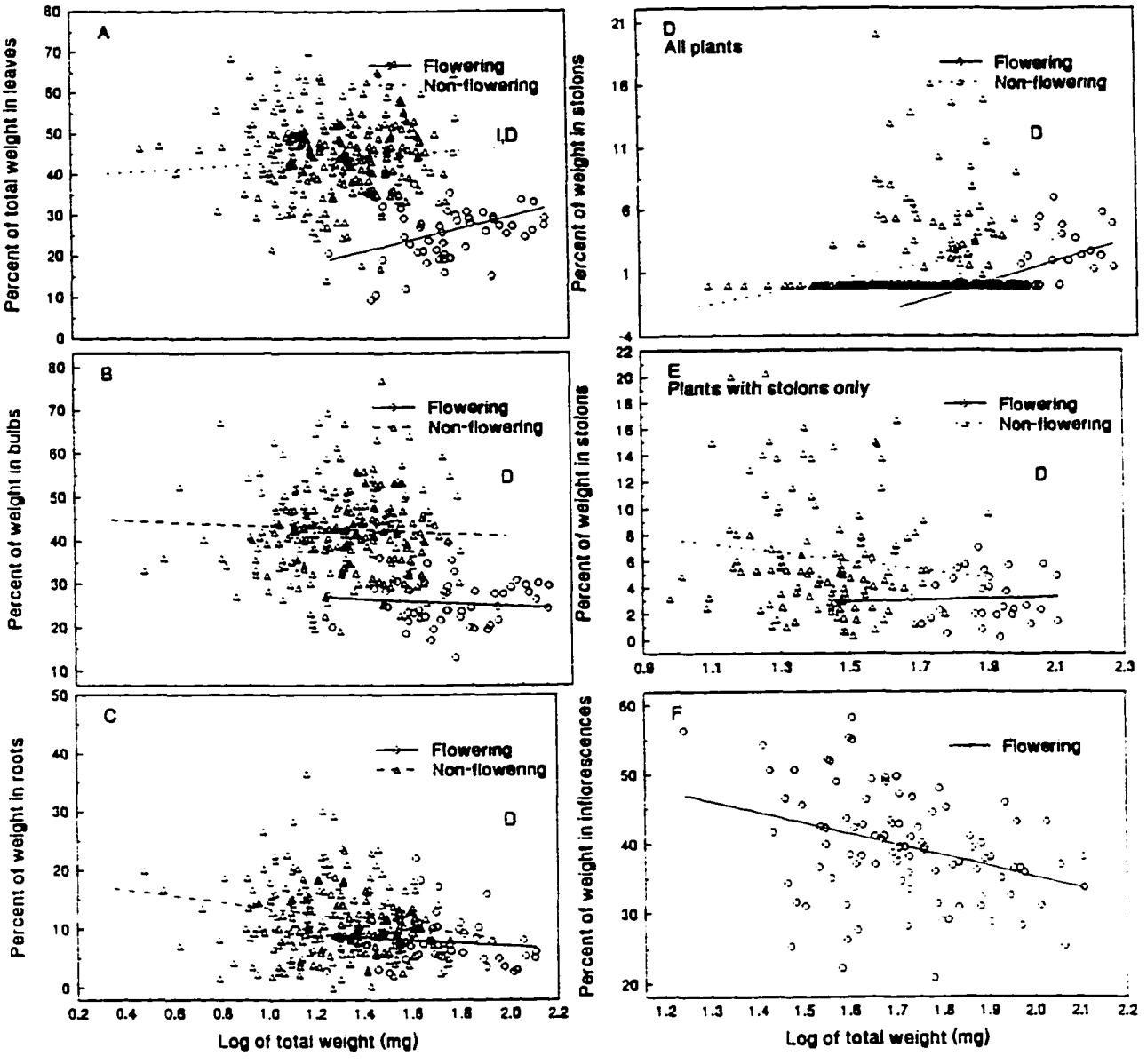


Figure 3. Plot experiment results: allocation to biomass of flowering and nonflowering arrowgrass corrected for total plant weight. Data are for the Yukon-Kuskokwim Delta in late July 1994. A 'D' indicates a significant difference in intercepts between the two groups, but not in slope: an 'I' indicates a significant interaction between flowering status and total nonreproductive weight. a). Percent of total weight in leaves vs. total weight. b). Percent of total weight in bulbs vs. total weight. c) Percent of total weight in roots vs. total weight. d). Percent of total weight in stolons vs. total weight for all plants. e). Percent of total weight in stolons vs. total weight for plants with stolons only. f). Percent of weight in inflorescences vs.total weight for flowering plants.

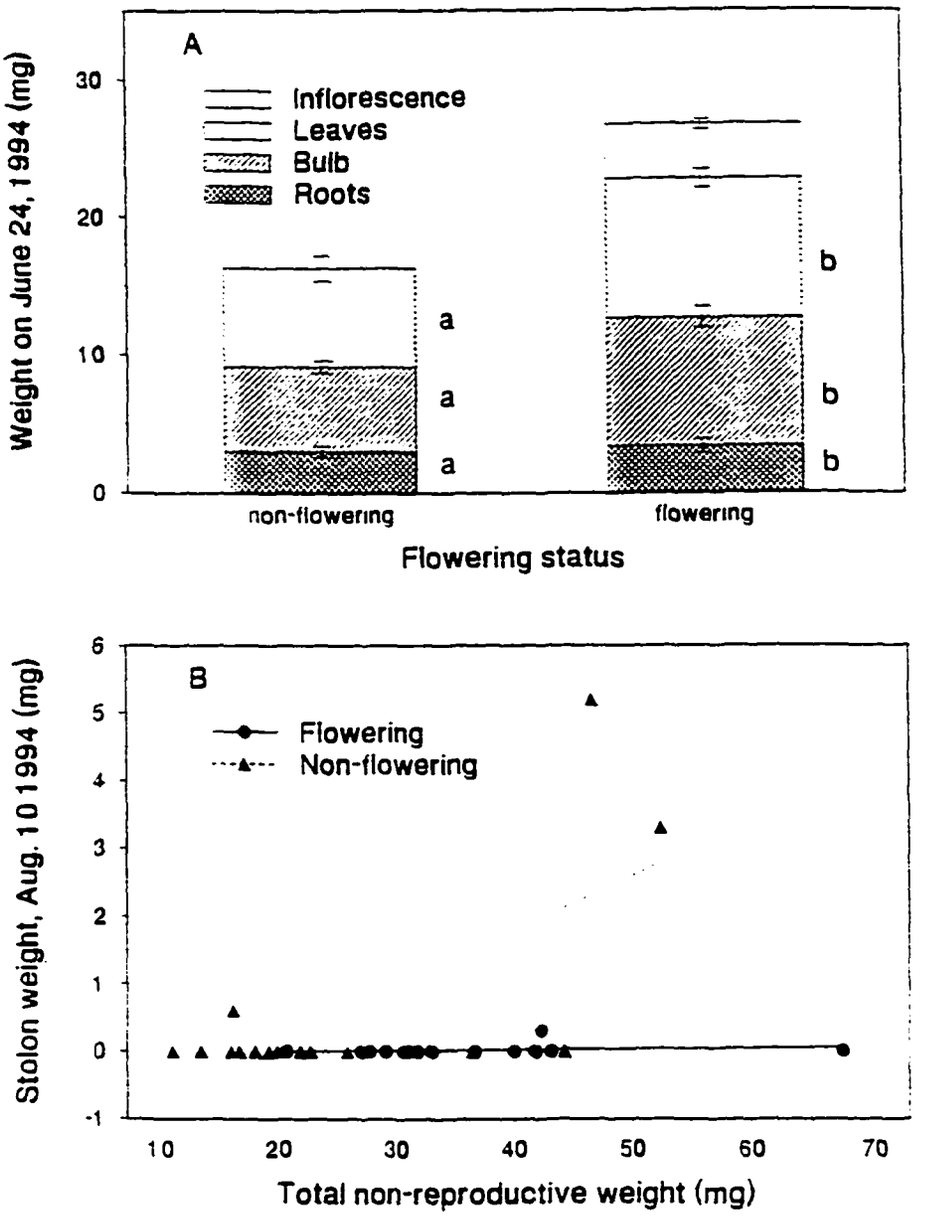


Figure 4. Flower tracking experiment: differences between flowering and nonflowering arrowgrass. a). Initial weights of flowering and nonflowering plants, 24 June, 1994. Different letters indicate a significant difference in weight, error bars are standard errors. b). Stolon weights by total nonreproductive weights for flowering and nonflowering plants on August 10, 1994.

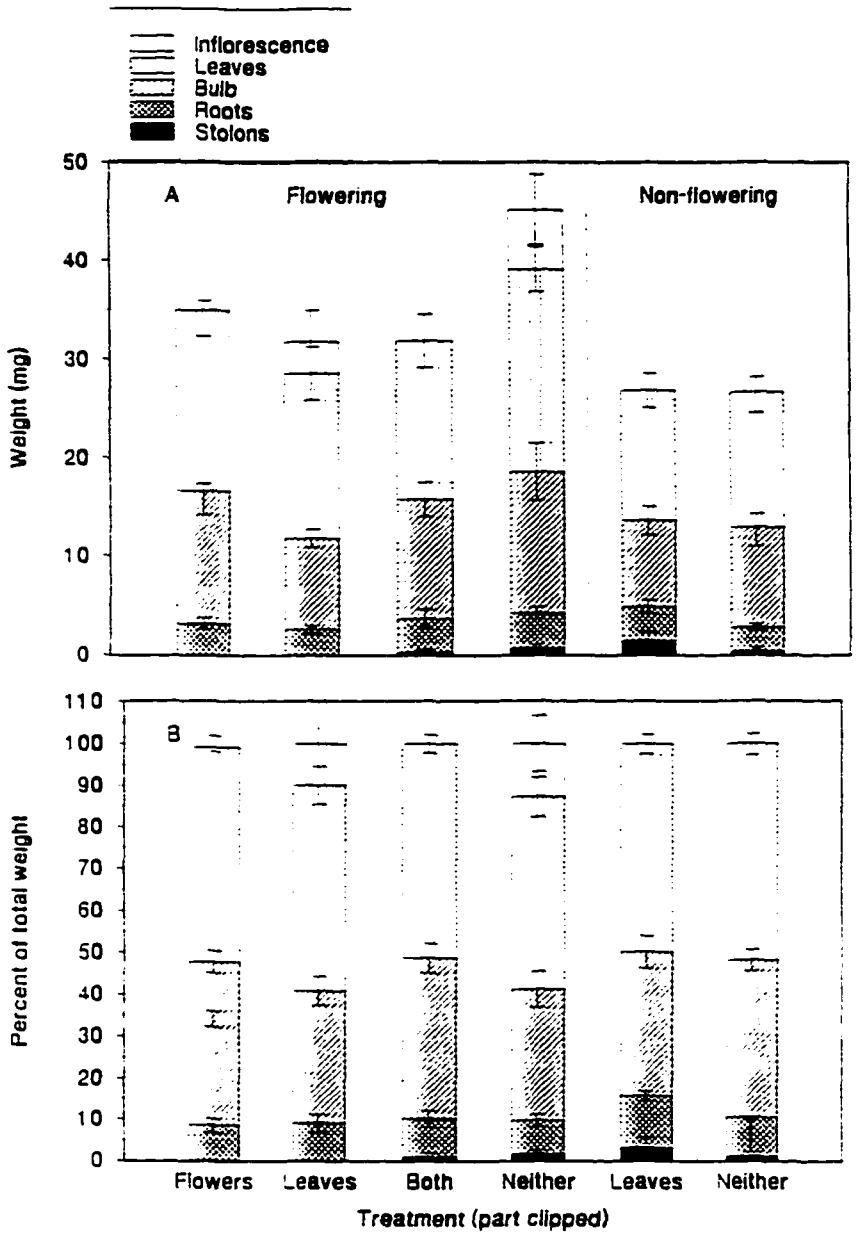


Figure 5. Clipping experiment: weight and biomass allocation of arrowgrass by treatment. Data are for 10 August 1994 on the Yukon-Kuskokwim Delta. a). Weights of plants in each treatment. b) Percent of total weight in plants of each treatment. Error bars are standard errors.

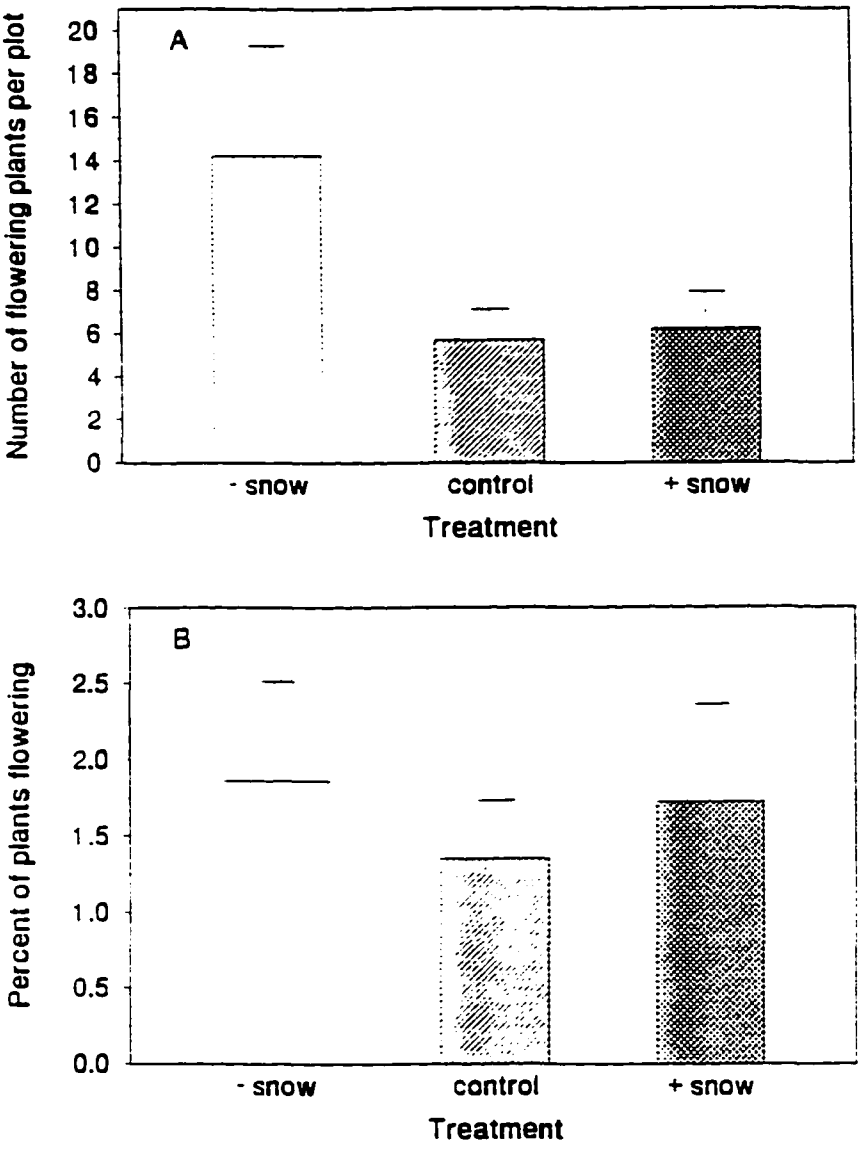


Figure 6. Results of the snow removal experiment. Data are for arrowgrass on the Yukon-Kuskokwim Delta on14 June, 1995. a) Number of flowering arrowgrass per plot for each treatment. b) Percent of arrowgrass flowering per plot in each treatment. Error bars are standard errors.

CHAPTER FIVE:

SYNTHESIS

GENERAL DISCUSSION

On the Yukon-Kuskokwim (Y-K) Delta, indirect effects of geese (*Branta*) on arrowgrass (*Triglochin palustris*) may have much larger effects than simple removal of biomass. Biomass removal has no detectable effect on population growth rate over 1 year, and little effect on plant size. Removal of biomass affects biomass allocation, but this allocation appears to have little effect on survival or reproduction. In contrast, at least three interactions appear to have large effects on both arrowgrass individuals and populations. First, geese modify the nutrient environment of both arrowgrass and its neighbors through feces deposition; the differential ability of plant species to respond to the addition of nutrients alters competition for light. This effect differs sharply from the effects of feces deposition on the grazing lawns on the subarctic salt marsh investigated by Jefferies and his co-workers (e.g. Bazely and Jefferies, 1985, 1989; Cargill and Jefferies, 1984). In the low-diversity systems at La Pérouse Bay, all plants were affected equally by herbivory, and thus there was little room for changes in competitive abilities. As a result, at La Pérouse Bay fertilization affected only nutrient cycling rates, and not interspecific competitive interactions (but see Hik et al., 1992). Results from both Chapter 2 and Chapter 3 show that in the relatively species-rich grazing system on the Y-K Delta, the role of fertilization in the system is more complex and that feces deposition does not increase productivity of at least one preferred forage species.

Goose selectivity for particular species results in a second interaction modification: from the perspective of arrowgrass, lower preference for other species may result in higher rates of

arrowgrass herbivory than may be predicted from rates of herbivory on each species. Results from Chapter 2 suggest that the combination of a decrease in ability to compete for light coupled with selectivity for arrowgrass may limit the expansion of arrowgrass in the *Carex* wet meadow community, despite its apparent ability to thrive there in the absence of geese. A third interaction, however, works in favor of arrowgrass: results from Chapter 3 suggest that the presence of *Salix* may lower visibility of arrowgrass and thus decrease grazing rates. The sum of these indirect effects has consequences at the population / community level: although neither population growth rates nor biomass differed between control plots and plots in which arrowgrass had been repeatedly clipped, excluding geese resulted in an increase in arrowgrass biomass.

Overall, the picture painted by this study of subarctic saltmarshes is consistent with views emerging from research on other saltmarshes (e.g. Ellison, 1987; Bertness and Shumway, 1993; Bertness and Hacker, 1994) : abiotic factors play a role in structuring the community (e.g. the range of arrowgrass is probably limited on the slough side by low nutrient availability and the physical effects of flooding), but they interact with biotic factors in complex ways. Furthermore, interactions between arrowgrass and other plants species should be viewed as lying along a continuum, depending on conditions. Neighboring species can act as competitors (with the level of competition depending on the presence of geese), but they can also have a positive effect on arrowgrass by reducing the probability of herbivory. The view of saltmarsh plant communities as simple systems governed almost entirely by a few abiotic factors is as inaccurate for slough levee vegetation on the Y-K Delta as for New England saltmarshes.

My study provides detailed information about how geese affect arrowgrass on an individual level, but it is still difficult to make predictions about consequences at the population level. Interactions between geese, arrowgrass and other species are manifested over different time

scales, and the time after which the results are viewed affect interpretation (Brown and Allen, 1989): if I had examined plants 5minutes after a grazing or clipping event, I probably would have reached different conclusions regarding the relative importance of direct and indirect effects. The direct effects are manifested both immediately (plant size and allocation) and over the course of a year (lower rates of survival and reproduction), while indirect effects become apparent over different time scales: weeks to months for changes in competition for light, months to years for feedbacks from the vegetation to future food availability to geese, and probably many years for any selection against flowering due to increased risk of herbivory. In contrast, my field measurements concentrated on within-season effects, and my grazing manipulation treatment involved very short times periods (10-30 minutes) and very small spatial scales (2.25 m^2). In addition, interactions between arrowgrass, other plants, and geese are probably dependent on intensity of grazing as well as frequency of grazing. For example, whether neighbours reduce grazing on arrowgrass may depend on length of time and intensity of grazing within a patch, while the size of arrowgrass should depend on the time since last grazing but also affects the probability of regrazing. In addition, if arrowgrass availability affects goose behaviour and movement (Sedinger and Raveling, 1988), this species will have a much larger effect on ecosystem functioning than its small size and small proportion of the biomass suggest . My results have implications not just for arrowgrass populations but also for goose populations: feces deposition is unlikely to readily result in increased productivity of arrowgrass in this habitat, and the relationship between grazing intensity / frequency and food availability is probably much more complex in the slough levee community than on the *Carex subspathacea / Puccinellia phryganodes* grazing lawns.

A major gap in our understanding of this system is our lack of knowledge of goose foraging behaviour. We have some knowledge of large scale foraging patterns and pecking rates

of cackling Canada (*Branta canadensis minima*) geese in different habitats (Sedinger and Raveling, 1986, 1988), and one study suggests changes in foraging behavior with changes in food availability, particularly arrowgrass (Sedinger and Raveling, 1988). We have, however, little understanding of how geese make 'decisions' on where to forage or how long to remain in a patch, or how exactly geese locate their forage species. More problematically, we do not understand the temporal and spatial scales over which such decisions are made. A much better understanding of goose foraging behavior is needed to predict changes in arrowgrass populations with goose population size, and thus link arrowgrass and goose populations directly. Foraging theory has been developed for situations where herbivores consume spatially dispersed, nonapparent plants (Senft et al., 1987; Spalinger and Hobbs, 1992), but understanding goose foraging on the Y-K Delta will require field observations and manipulations specifically designed to elucidate goose behaviour over several spatial scales.

In addition to problems inherent in combining results over different temporal and spatial scales, a second scale-related problem exists in predicting population level consequences. All of the experimental chapters have focused on mean effects over plots or over many plants, whereas associational refuges and increased competition following fertilization both involve small-scale spatial interactions. In other words, I have completely ignored any spatial structuring in the community, despite evidence for its importance in other communities (Harper, 1977; Tilman, 1994). To generate hypotheses concerning potential consequences of goose-arrowgrass-competitor interactions and the importance of spatial structure in regulating these interactions, I have produced a simple, spatially explicit model.

A MODEL

Purpose

Celluiar automata models are conceptually simple. They consist of an array of cells (1, 2 or 3-dimensional), each of which can assume a small number of discrete states. A cell may represent one individual of a given species or be 'empty'. Changes in the state of each cell over each time step depend on its own state and the state of neighboring cells, and follow simple transition rules. The transition rules are applied to the grid of cells for successive iterations. Even the most simple cellular automata models can result in complicated spatial and temporal dynamics and that patchiness (spatial heterogeneity) can be generated even when starting with spatial homogeneity (review in Phipps, 1992).

Cellular automata models have several advantages. First, they are spatially explicit: each individual is located at a specific location on the grid, and 'interacts' only with its neighbors, which can be defined at any scale. For a small and sessile organism like arrowgrass, the immediate surroundings are likely to be much more important than mean conditions over a large area. Similarly, the ability of geese to locate arrowgrass within a patch is likely to be affected by the distribution of other species as well as by mean abundance. The interactions themselves have a spatial component: neighborhoods can be varied in size, or, in this case, the spatial distribution of geese affecting the plants can be varied. In addition the resulting populations can be examined both in terms of numerical variation over time, and over space. Second, these models lend themselves well to the investigation of qualitative (rather than quantitative) changes, such as the inclusion of associational refuges (AR's).

This model is *not* designed to make specific predictions about arrowgrass population dynamics, which are likely to be highly dependent on the specific rules used (Phipps, 1989). Rather, it should be viewed as a tool to simultaneously examine consequences of several of the results from the experimental work, generate new hypotheses, and point out areas for future research emphasis.

Model description

In this model, the 'universe' consists of grids of 39 by 39 square cells, with a one cell wide border to reduce edge effects (Fig. 1).

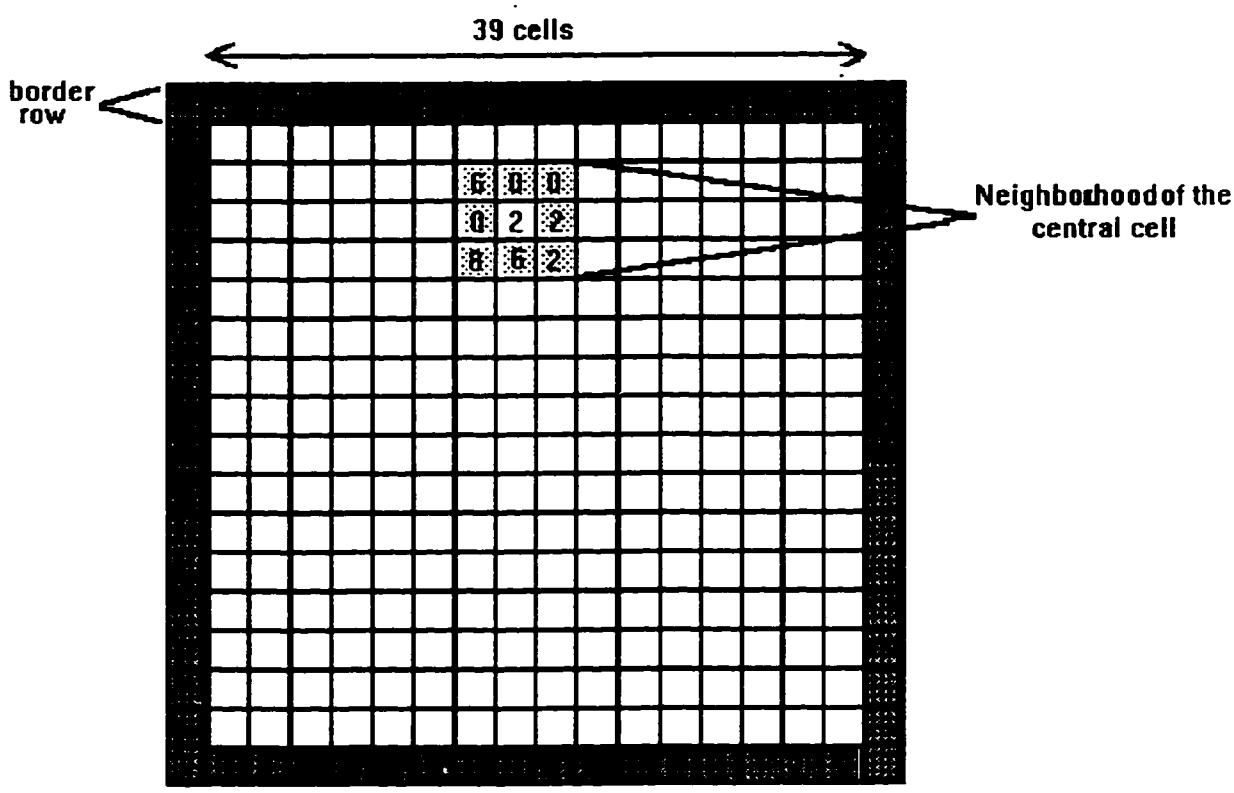


Figure 1. Schematic representation of the vegetation grid. The stippled area represents the neighbourhood of the center cell.

There are two such grids. The first is the vegetation grid, in which cells can assume one of nine different states: empty, four possible states of arrowgrass (combinations of grazed and ungrazed, large or small), and four possible states of other plants (combinations of edible or non-edible, large or small) (see Table 1 for details). For each cell, its neighborhood is defined as the eight surrounding cells (Fig. 1). The grid is represents an area of approximately 1.5 m * 1.5 m. The second grid is the goose grid, in which cells can assume one of two possible states: goose present (1) or goose absent (0).

Table 1. Definition of cell states in the vegetation grid, and effects of "grazing" on each state. Grazing occurs when the corresponding cell in the goose grid is in state'1', and the change in state represents the 'within year transition'. 'Competitor' here refers to species other than arrowgrass, and 'nutrients' to fertilization through nutrient deposition. All plants are ungrazed at the beginning of each generation.

State	Definition	State after grazing	Explanation
0	Empty cell	0	Empty cells are not affected
1	Small grazed arrowgrass	---	---
2	Small ungrazed arrowgrass	1	Arrowgrass is grazed
3	Large grazed arrowgrass	---	---
4	Large ungrazed arrowgrass	3	Arrowgrass is grazed
5	Small edible competitor	0	Plant is consumed
6	Small inedible competitor	8	Nutrients lead to growth
7	Large edible competitor	5	Plant is partly consumed
8	Large inedible competitor	8	No change

During the within-year transition, the goose grid is placed on top of the vegetation grid, resulting in the first transition of the vegetation grid (Fig. 2); this can be thought of as the direct effect of goose presence.

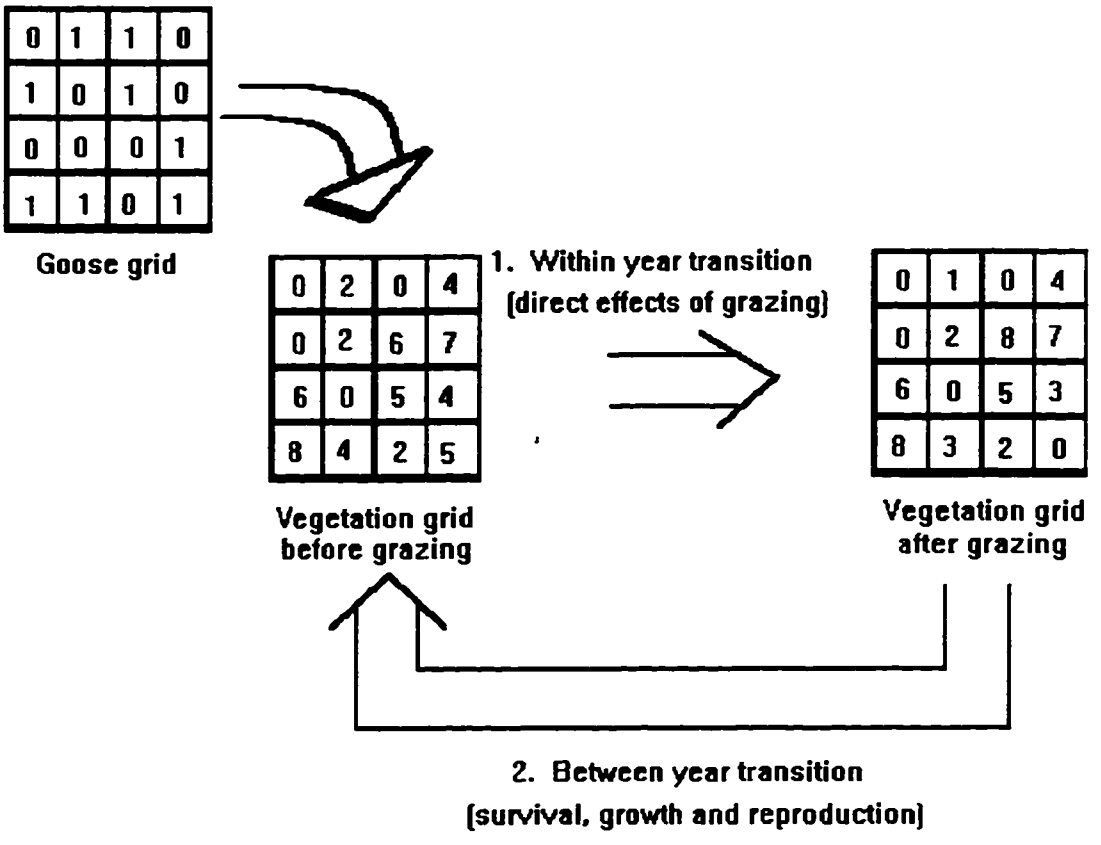


Figure 2. Schematic representation of the model. Each loop represents one generation.

In the simplest version of the model, the change in state of each cell in the vegetation grid during this transition is dependent only on the state of the goose grid cell placed on top of it: a '0' (no goose) results in no change, while a '1' results in ungrazed arrowgrass becoming grazed, edible

plants becoming empty cells, and non-edible cells growing (see Table 2 for details). The within-year transition is followed by the between-year transition, in which the change in vegetation cells is dependent on its own state, the state of the neighbors (all cells in the neighborhood), and the state of the goose grid in the neighborhood (Table 2). The transition rules are deterministic summation rules, where the behavior of each cell depends on sums of states of neighboring cells (Table 2). The within-year transition plus between-year transition together represent one arrowgrass generation.

Initial conditions for the vegetation grid are similar for all runs: 1/3 of the cells contain small arrowgrass, 1/3 contain small competitors, and 1/3 are empty. Dynamics of the arrowgrass population are faster than those of the populations of competitors; arrowgrass changes state more easily than competitors do.

The model was run for up to 100 generations (iterations) using a newly generated goose grid in each generation. Arrowgrass population size was recorded after 5, 10, 25, 50 and 100 generations, and the run was stopped when the arrowgrass population went extinct. Once the population reached approximately 15 individuals, it tended to persist for a long time, possibly due to edge effects. I therefore defined 'extinction' as 15 individuals or fewer. Because initial conditions for each run were probabilistic (e.g. a random distribution of arrowgrass) for each set of conditions each model was run 10 times to generate mean behaviors of the arrowgrass population. I also examined the vegetation grids for spatial patterning in the arrowgrass population.

Table 2. General rules for the between-year transition. Exact values for summation rules depend on the particular version of the model, and are here given simply as 'min' or 'max'. Ncell (x,y) refers to vegetation grid cells in the neighbourhood of the target cell in state x or state y. Gcell refers to goose grid cells corresponding to the neighbourhood of the target cell.

Initial state		New state	General rule	Explanation
0	┌	2	If ΣNcell (1,2,3,4) > min	Many nearby arrowgrass leads to colonization by small arrowgrass
	├ else	5 or 6	If ΣNcell((5,7) or (6,8))> min	Many nearby competitors leads to colonization by competitors
	└ else	0		Otherwise the cell stays empty
1	┌	0	If ΣNcell(5,6,7,8)>min	If there are many competitors small grazed arrowgrass dies
	└ else	2		Otherwise it becomes ungrazed
2	┌	0	If ΣNcell(5,6,7,8)>min	If there are many competitors small ungrazed arrowgrass dies
	├ else	4	If ΣNcell(5,6,7,8)<max & ΣGcell>max	If there are few competitors and many feces it grows
	└ else	2		Otherwise it doesn't change
3	┌	0	If ΣNcell(5,6,7,8)>min	If there are many competitors large grazed arrowgrass dies
	├ else	4	If ΣNcell(5,6,7,8)<max & ΣGcell>max	If there are few competitors and many feces it stays large
	└ else	2		Otherwise it becomes small
4	┌	0	If ΣNcell(5,6,7,8)>min	If there are many competitors large ungrazed arrowgrass dies
	└ else	4		Otherwise it stays large
5 or 6	┌	0	If ΣNcell(5,6,7,8)>min	If there are many competitors a small competitor dies
	├ else	7 or 8	If ΣNcell(5,6,7,8)<max	If there are few competitors it grows
	└ else	5 or 6		Otherwise it stays small
7 or 8	┌	0	If ΣNcell(5,6,7,8)<max	If there are many competitors a large competitor dies
	├ else	5 or 6	If ΣNcell(5,6,7,8)<max	If there are a medium number it becomes small
	└ else	7 or 8		Otherwise it stays large

Rationale for transition rules

The number of potential combinations for transition rules multiplies quickly, and it is impossible to examine the effect of each one individually. The transition rules used for the arrowgrass are derived directly from the experimental chapters (Table 2), and neighborhoods (three by three cells) represent 10 by 10-cm plots. The transition rules for competitors were based on the assumption that population dynamics are slow relative to those for arrowgrass, but the competitors do not represent any particular real species.

Model versions

Five versions of the model were run, each including different assumptions about interactions (see Table 3 for details). The basic model included no advantages of goose presence: the only effect of geese on arrowgrass is reduced survival and reproduction through reduced size following grazing or increased competition following fertilization. The 'edible competitors' model assumed that some other plants are edible and also vulnerable to grazing; the benefit of goose presence is thus expressed through reduced competition. The 'indirect effects' model included two results from Chapter 3: that fertilization reduces arrowgrass size only if it is not clipped, and that stolon production increases under fertilization only when neighbors are clipped (Table 3). Thus in this model one aspect of the presence of geese (fertilization) had both a potentially negative and a potentially positive effect on arrowgrass. The 'Associational Refuge (AR) model' included effects from the indirect effects model but assumed that arrowgrass is somewhat protected from grazing

by the presence of other plants in the neighborhood (Table 3). The 'complete model' included edible competitors, indirect effects, and AR's.

Table 3. Versions of the model. Ncell (x,y) refers to vegetation grid cells in the neighbourhood of the target cell in state x or state y. Gcell refers to goose grid cells corresponding to the neighbourhood of the target cell.

Name of model version	Additional features
Base model	All competitors are inedible (state 6 or 8)
Edible competitors	Initially, edible competitors (states 5 and 7) are half of all competitors
Indirect effects	1. Ungrazed arrowgrass (states 2,4) die or are reduced in size by fertilization (ΣGcell>min); grazed arrowgrass are not affected. 2. If the neighborhood is fertilized (ΣGcell>min), fewer arrowgrass are needed (ΣNcell(1,2,3,4) for an empty cell to be colonized by arrowgrass.
Associational Refuge (AR)	Indirect effects features + a '1' in the goosegrid leads to grazing only if ΣNcell(5,6,7,8)< max
Complete model	Edible competitors features + Indirect effects features + AR features

Parameters investigated

1. Grazing intensity

For each version of the model, I examined the effect of grazing intensity by varying the probability of goose grazing (percentage of cells in the goose grid in state 1) between 0%, 10%, 25%, 50%, 75%, 90%, and 100%. A given level of grazing was maintained throughout the run.

2. Temporal effects

I examined whether the conclusions regarding results of each model are dependent on the time at which arrowgrass population size is examined, by comparing the results after 5, 10, 25, 50 and 100 years.

3. Spatial distribution of geese.

For each version of the model and for each grazing intensity, the distribution of geese was either random or patchy (the goose grid was 'seeded' with 1's and patches of 1's were created around these). The same levels of grazing intensity (percent goose grid cells in state 1) were used for both versions; this allowed me to examine whether spatial distribution of geese *per se*, rather than grazing intensity, affected arrowgrass population dynamics.

Model Results

Results for the basic model, which includes only negative effects of goose presence on arrowgrass, were straightforward (Fig.3): a linear decline in arrowgrass population size with an increase in grazing intensity. For this model, there was no difference in overall pattern between the version with random geese distributions (Fig. 3a) and with patchy geese distributions (Fig.3b). However, even under these conditions the arrowgrass population displayed patchiness at all levels of grazing intensity (Fig 4).

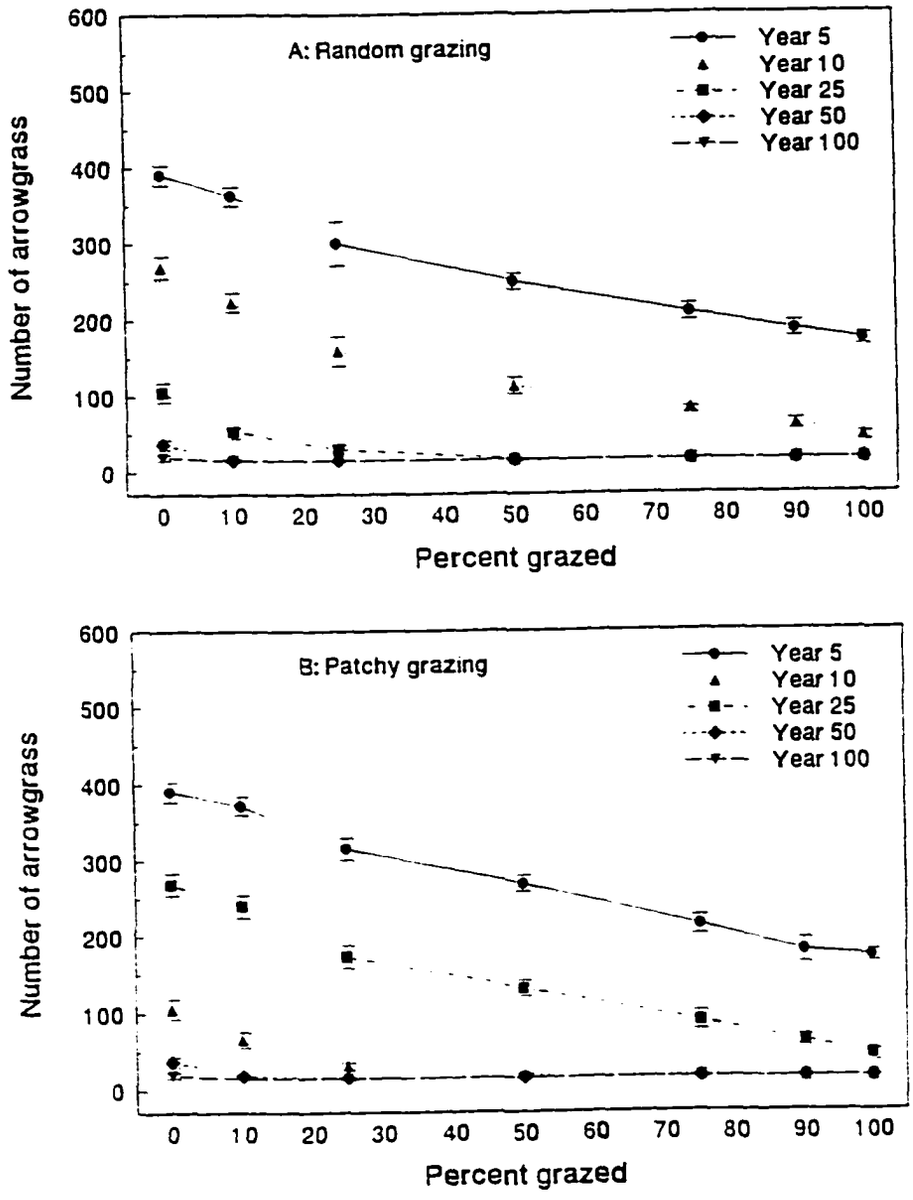
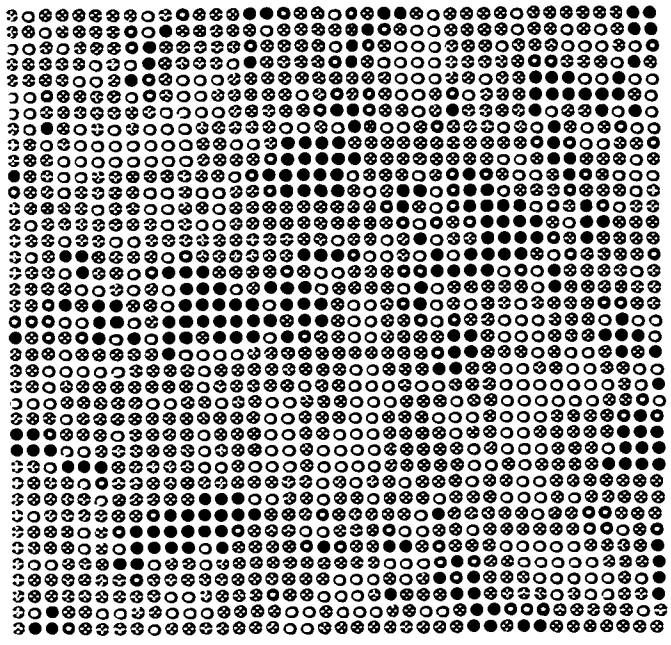


Figure 3. Results of the basic model. Error bars are standard errors of the mean from 10 runs of the model under each combination of percent grazed and year (generation). Arrowgrass was considered to occur when population size reached 15. A) Results of the model under a random goose distribution. B) Results of the model under a patchy goose distribution.

A



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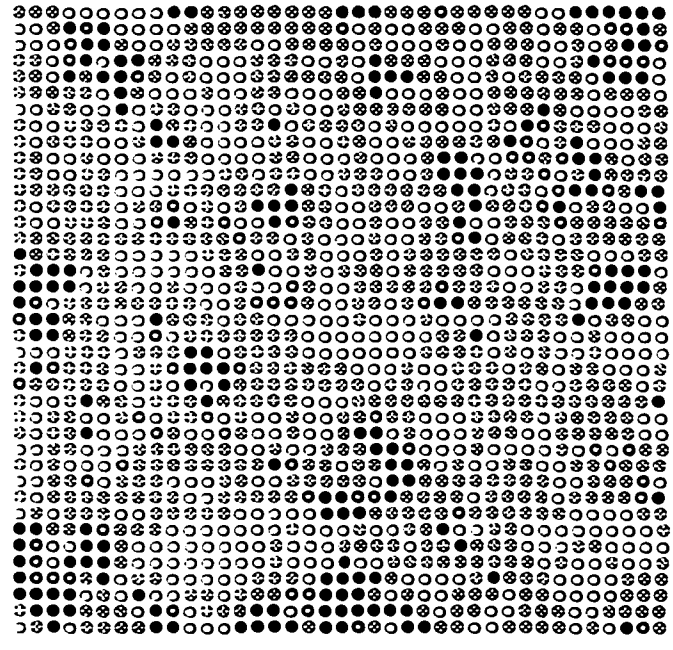


Figure 4. Examples of the vegetation grid under the basic model. These grids represent the vegetation after five years under 25% grazing at the beginning of a generation (no grazed plants present). ● = a large arrowgrass, ✪ = a small arrowgrass, ⊗ = an inedible competitor; ○ = an empty cell. A) An example under random distribution of geese. B) An example under patchy distribution of geese.

In the 'edible others' model the decline in arrowgrass population with an increase in grazing intensity was not linear: it appeared to reach a plateau between 25% and 75% grazing intensity, at least from generation 10 to generation 50 (Fig. 5). This plateau was more pronounced in the patchy grazing (Fig. 5a) than in the random grazing version (Fig. 5b), but the overall pattern was still very similar for the two versions. In addition, the pattern of change over time differed for different grazing intensities: whileat low levels of grazing there was a gradual decline in arrowgrass population, at 50% and 75% grazing the population was stable between five and 10 generations. Again, the distribution of arrowgrass was patchy, although the distribution of competitors and empty cells appeared to be less patchy than under the base model (Fig. 6).

In the 'indirect effects' model the patchy grazing and random grazing models differed in overall pattern of changes in arrowgrass population size with grazing intensity (Fig. 7). Under random grazing pattern, there was a linear decline between 0 and 25% grazing, a plateau between 25% and 50%, followed by another decline to 100%. In contrast, the patchy grazing pattern resulted in a linear decline between 0% and 50%, with a plateau to 100%. Examples of the vegetation grids after five years are shown in Fig. 8.

Adding AR's to the indirect effects model resulted in a gradual decline in population size with an increase in grazing intensity for the random goose distribution version, but a gradual decline until 50% grazing followed by a plateau until 90% grazing for the patchy goose distribution version (Fig. 9). Patchiness is particularly distinct in this model (Fig. 10). In the 'complete' model, a gradual decline with grazing intensity was evident only after > 50 generations (Fig. 11). After 5, 10, and 25 generations there was no difference in arrowgrass population size between 0, 10, 25, and 50% grazing, with a strong decline only between 75% and 100%. There was also a different pattern of change over time for different grazing intensities: although for zero,

five, and 25% grazing there was a gradual decline in population size, at 50, 75, and (for the random grazing model) 90% grazing there was an increase in population size between five and 10 generations. Once again, spatial patterns were distinct for arrowgrass, although not for other states (Fig. 12).

Model Discussion

For every single model, an increase in grazing intensity eventually results in a decrease in arrowgrass population, as evidenced by the numbers for the 100^{th} generations. The only model that suggests a linear decline with grazing intensity is the base model, in which no effects of geese other than decreased survival and increased competition exist. The plateaus and even increases in population at intermediate levels of grazing (and for the first 50 generations) upon the addition of other feedbacks from grazing suggest that we should not expect linear decreases in population size with increases in grazing intensity in real life. In fact, the model predicts initial increases followed by decreases in population size under some conditions. The change in population between 25% and 50% grazing, the most common range at the moment on the YK Delta, is particularly unstable from version to version. In addition, the pattern of change with grazing intensity differs between the random grazing and patchy grazing models for those which include 'indirect effects'. This implies that not just the mean level of grazing, but foraging behaviour within a patch will affect arrowgrass populations.

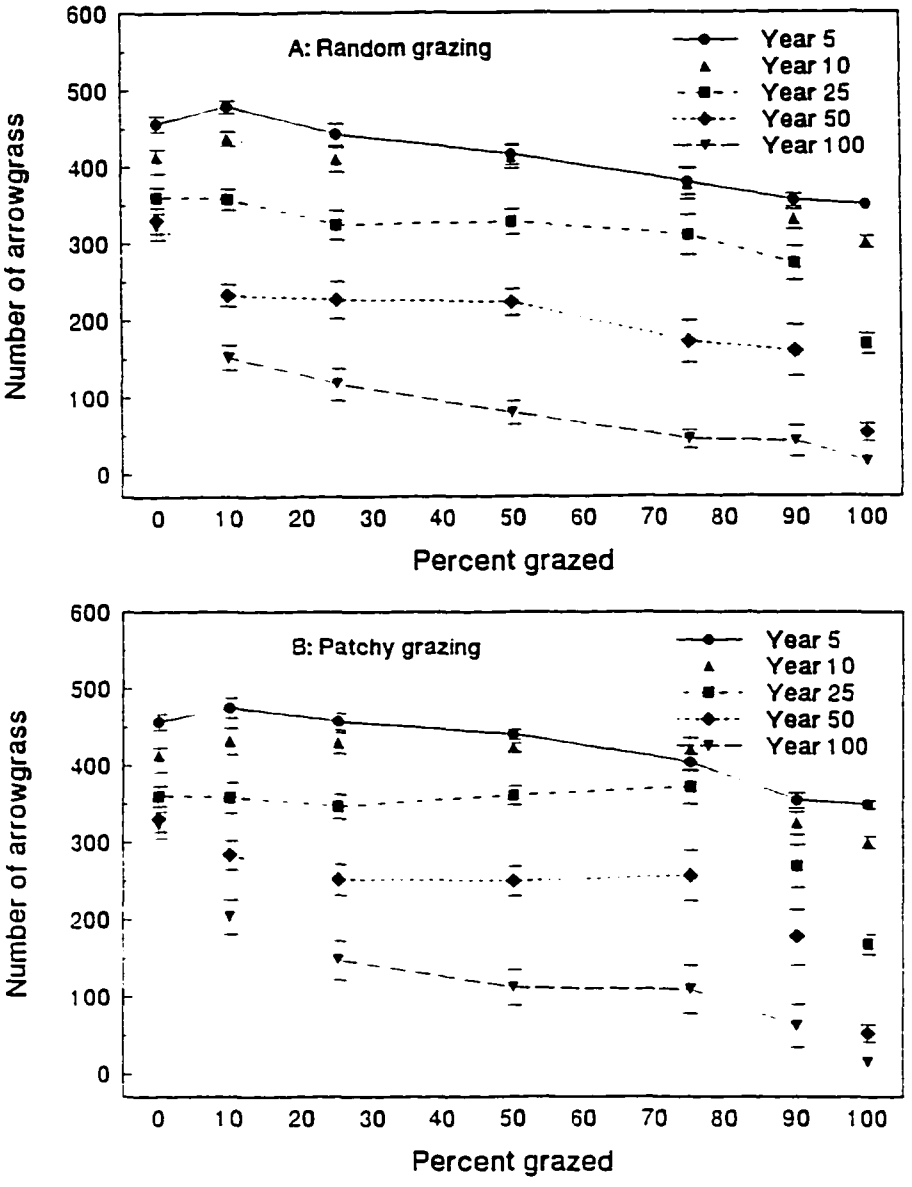
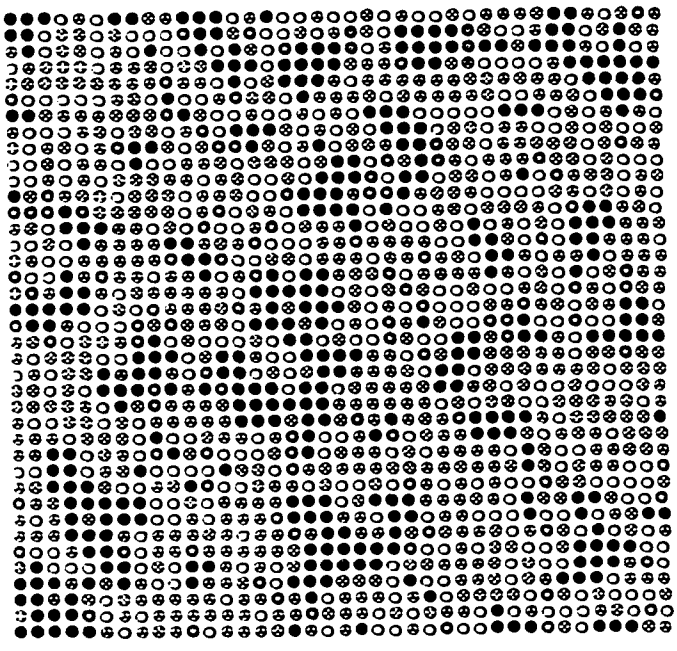


Figure 5. Results of the edible competitors model. Error bars are standard errors of the mean from 10 runs of the model under each combination of percent grazed and year (generation). Arrowgrass was considered to occur when population size reached 15. A) Results of the model under a random goose distribution. B) Results of the model under a patchy goose distribution.

A



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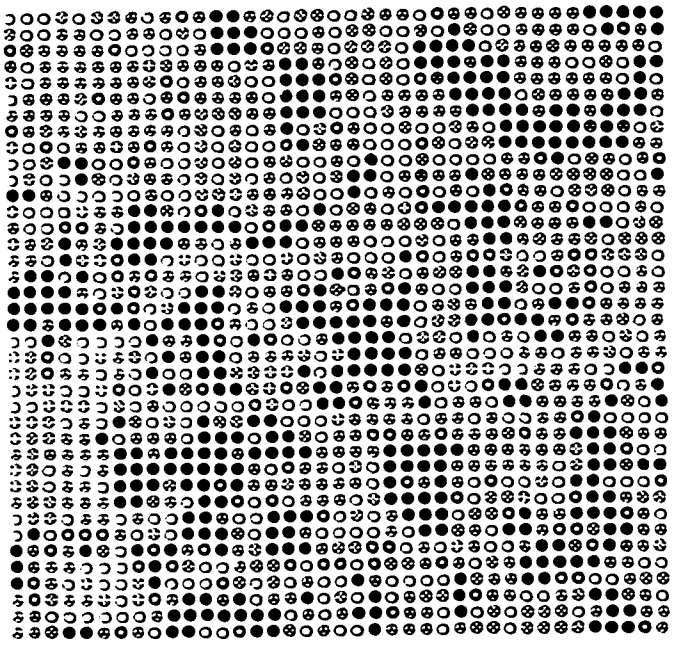


Figure 6. Examples of the vegetation grid under the edible competitors model. These grids represent the vegetation after five years under 25% grazing at the beginning of a generation (no grazed plants present). ● = a large arrowgrass, ✪ = a small arrowgrass, ⊗ = an inedible competitor, ⊜ = an edible competitor, ↄ = an empty cell. A) An example under random distribution of geese. B) An example under patchy distribution of geese.

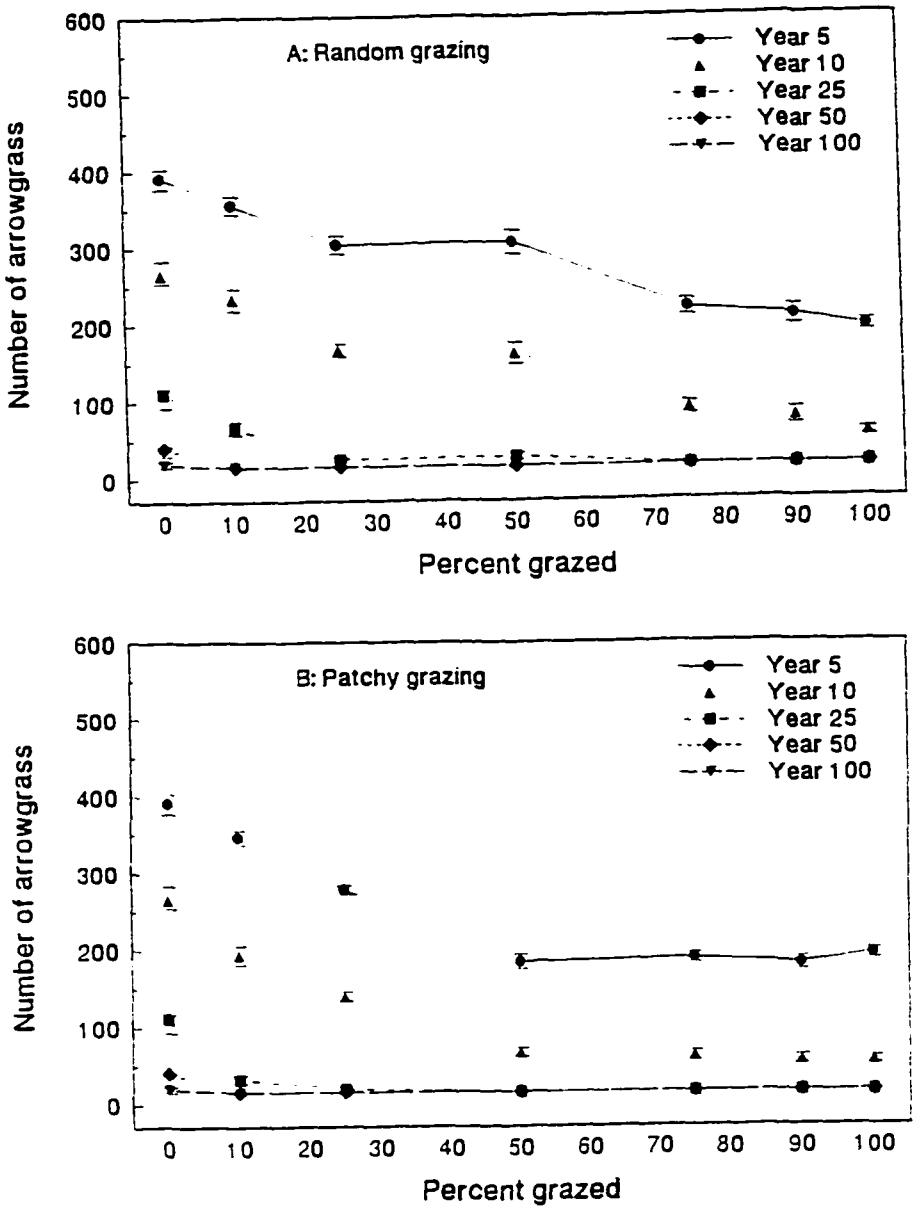
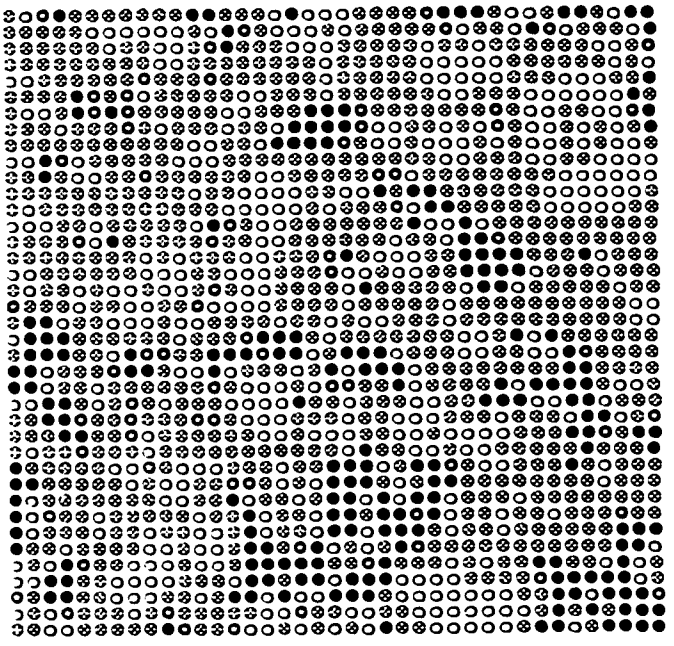


Figure 7. Results of the indirect effects model. Error bars are standard errors of the mean from 10 runs of the model under each combination of percent grazed and year (generation). Arrowgrass was considered to occur when population size reached 15. A) Results of the model under a random goose distribution. B) Results of the model under a patchy goose distribution.

A



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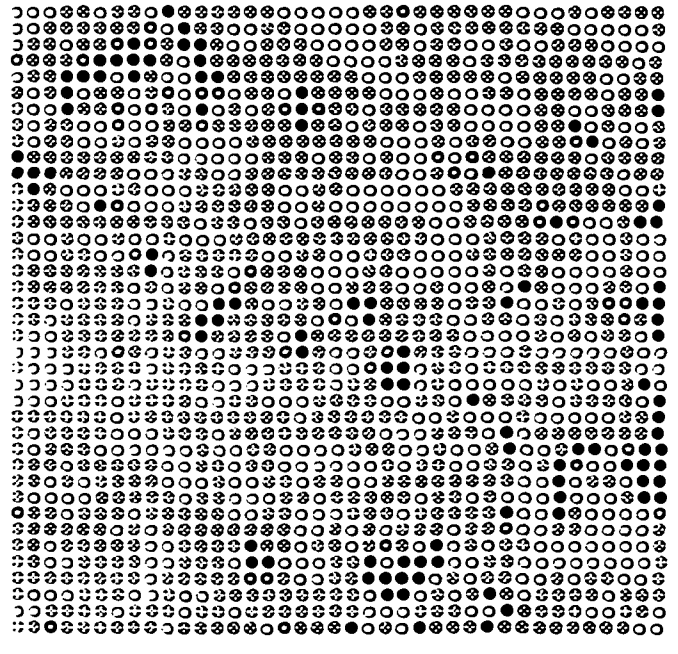


Figure 8. Examples of the vegetation grid under the indirect effects model. These grids represent the vegetation after five years under 25% grazing at the beginning of a generation (no grazed plants present). ● = a large arrowgrass, ✪ = a small arrowgrass, ⊗ = an inedible competitor, ⊜ = an edible competitor. ↄ = an empty cell. A) An example under random distribution of geese. B) An example under patchy distribution of geese.

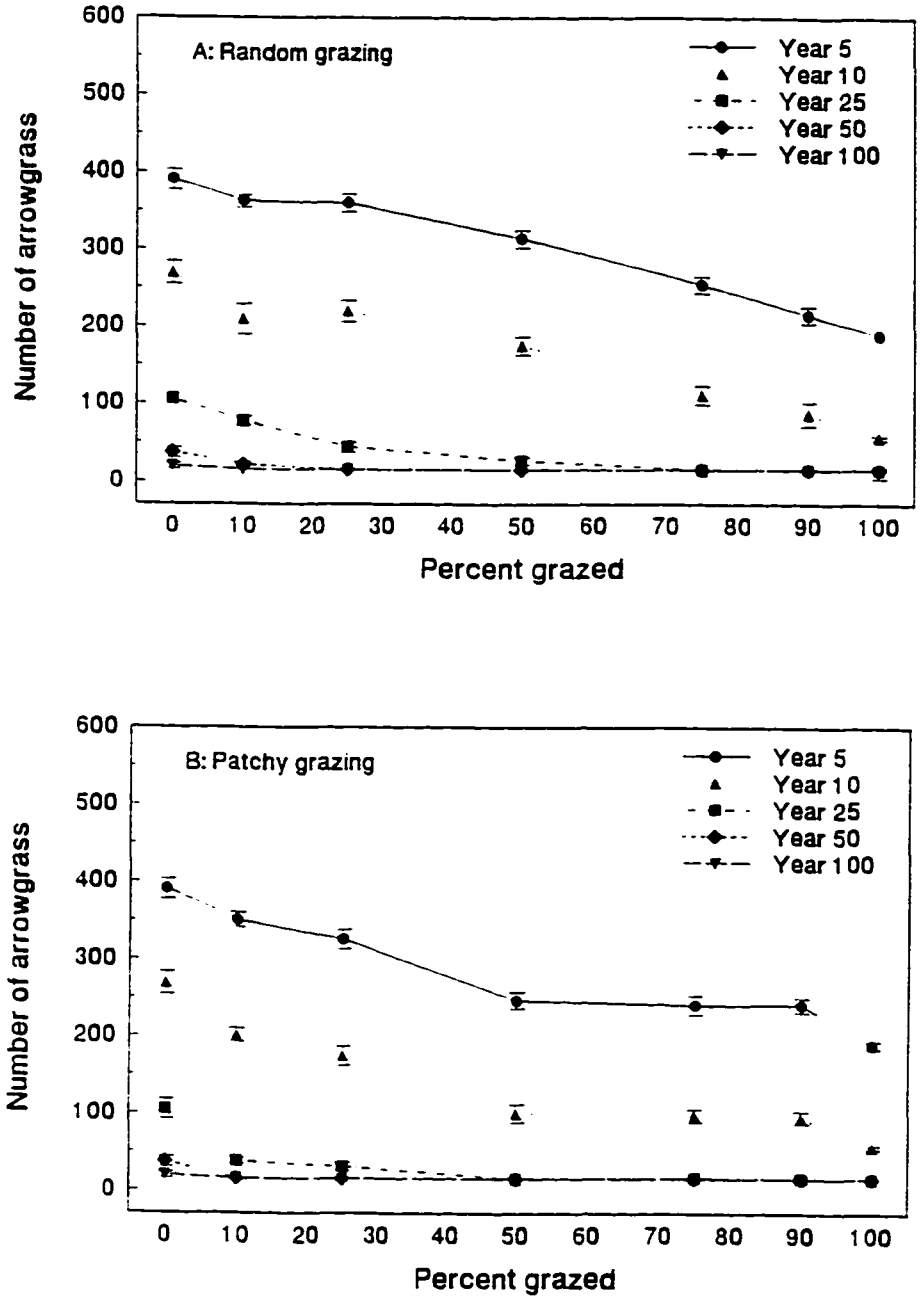
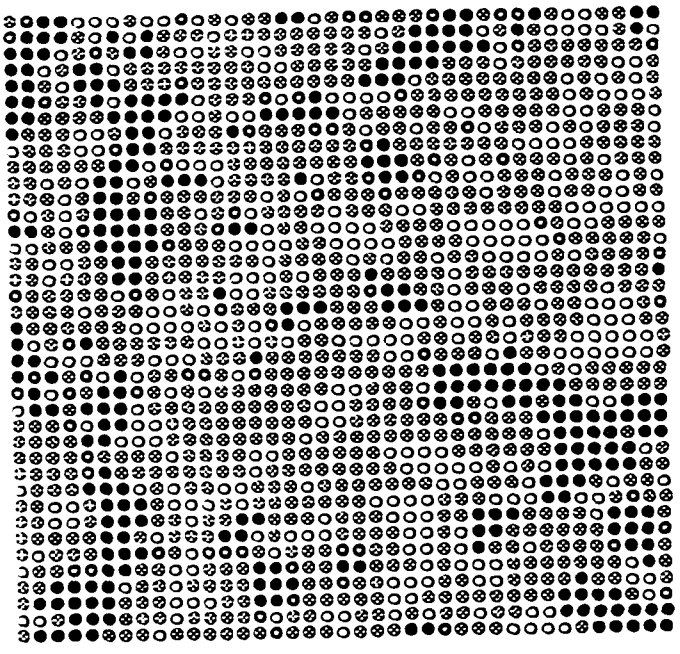


Figure 9. Results of the associative refuge model. Error bars are standard errors of the mean from 10 runs of the model under each combination of percent grazed and year (generation). Arrowgrass was considered to occur when population size reached 15. A) Results of the model under a random goose distribution. B) Results of the model under a patchy goose distribution.

A



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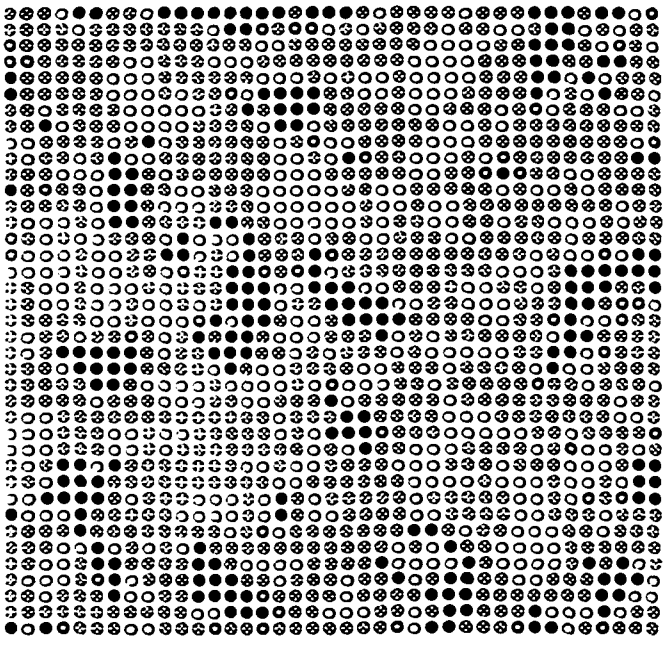

Figure 10. Examples of the vegetation grid under the associative refuge model. These grids represent the vegetation after five years under 25% grazing at the beginning of a generation (no grazed plants present). ● = a large arrowgrass, ✪ = a small arrowgrass, ⊗ = an inedible competitor, ⊛ = an edible competitor, ↄ = an empty cell. A) An example under random distribution of geese. B) An example under patchy distribution of geese.

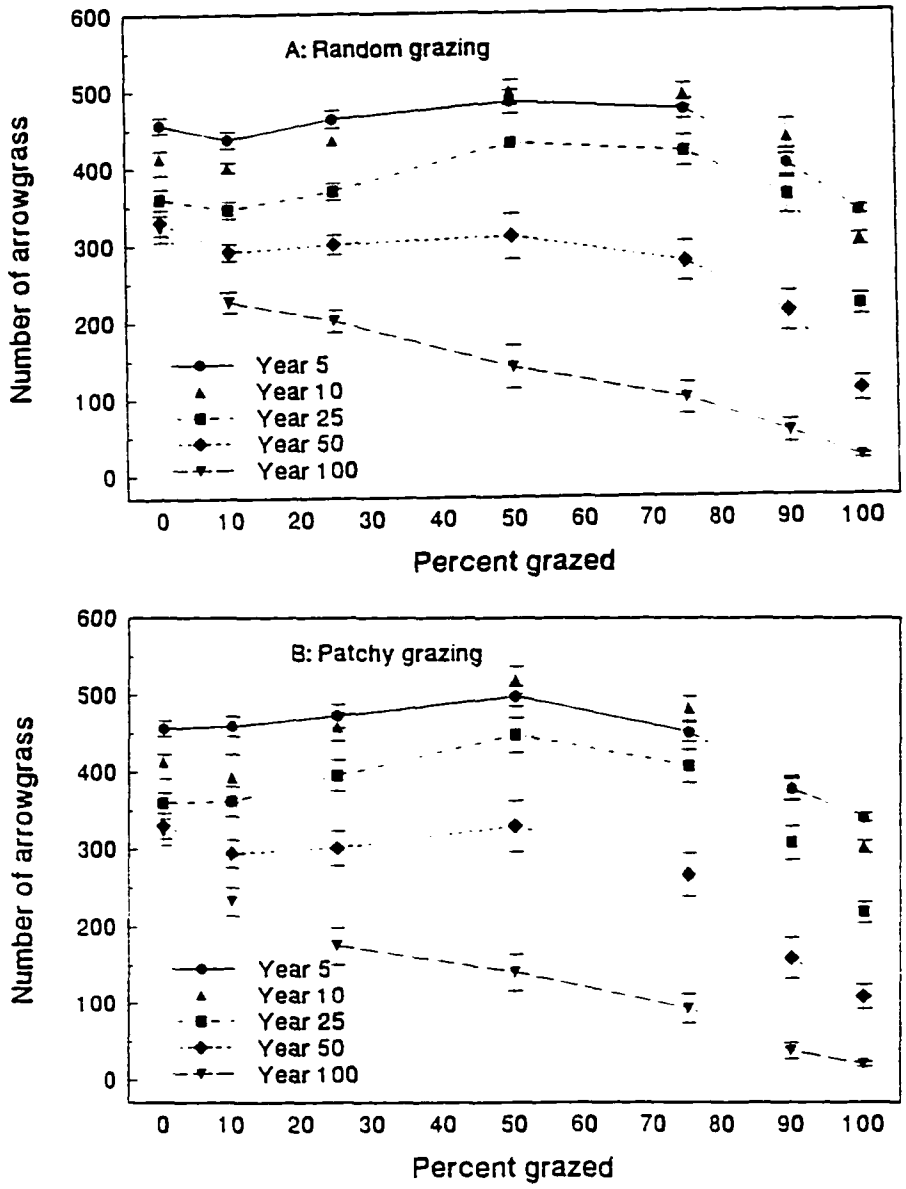

Figure 11. Results of the complete model. Error bars are standard errors of the mean from 10 runs of the model under each combination of percent grazed and year (generation). Arrowgrass was considered to occur when population size reached 15. A) Results of the model under a random goose distribution. B) Results of the model under a patchy goose distribution.

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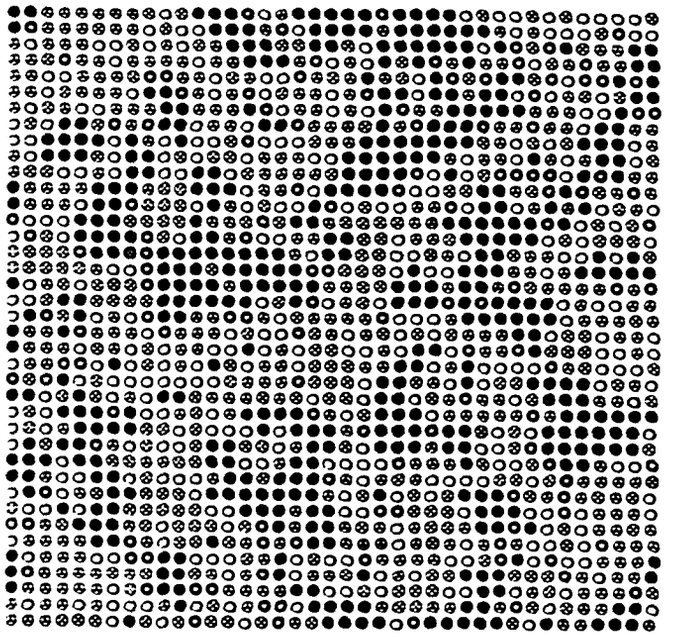

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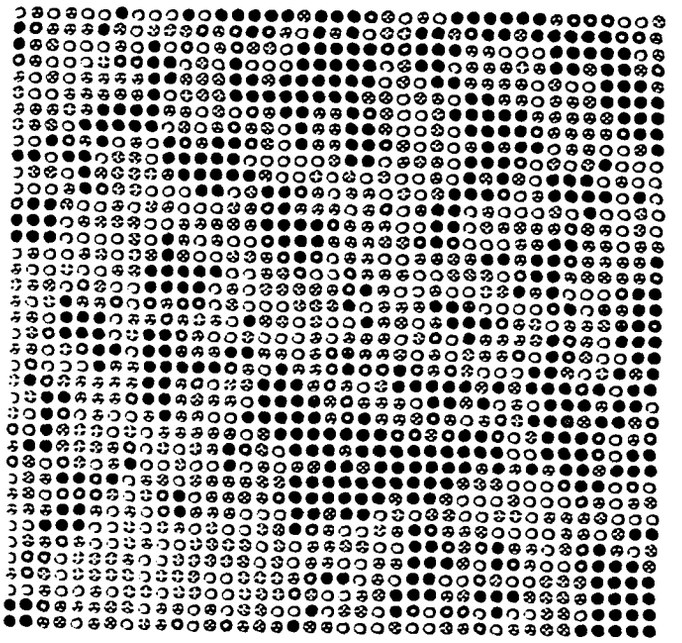

Figure 12. Examples of the vegetation grid under the complete model. These grids represent the vegetation after five years under 25% grazing at the beginning of a generation (no grazed plants present). ● = a large arrowgrass, ✪ = a small arrowgrass, ⊗ = an inedible competitor, ⊘ = an edible competitor, ○ = an empty cell. A) An example under random distribution of geese. B) An example under patchy distribution of geese.

The time (number of generations) after which I examine the results affects my conclusions: on examining only the 100th generation, I would conclude that all models result in a gradual decline in arrowgrass population with increase in grazing intensity, while an examination after 10 years would suggest that for the models including AR's, there is no effect or a positive effect of increased grazing.

Last, all of the model versions result in patchy distributions of arrowgrass, consistent with Phipps' Neighborhod Coherence Principle, which states that a state existing at a particular site tends to impose itself upon neighbouring sites, leading to local coherences (Phipps, 1989, 1992). In real life, for arrowgrass this patchiness is often seen at a very small scale (0.5 m^2; Chapter 3), and it is quite obvious at larger scales (10's of meters; *personal observation*). These models suggest that this patchy distribution could have resulted simply from the local interactions between arrowgrass, geese, and its neighbours, without any underlying environmental heterogeneity. Of course it is likely that outside factors such as soil heterogeneity played a role as well, but they may not be necessary for patchiness to emerge.

There are, of course, some major caveats in this model. Probably the biggest one is that grazing intensity was kept constant from year to year; not only is it likely to vary in real life, but geese are unlikely to spend much time on severely depleted patches when 'full' patches are available. In addition, the competition parameters are based on very limited experimental data. This in itself points out a large gap in my understanding of arrowgrass: although I can draw inferences about competition for light based on effects of clipping neighbours, I have no good quantitative information on competition.

Conclusions and Directions for Future Research

In general, the results from the model back up the conclusions I reached based on experimental results: the interactions between geese, arrowgrass and its neighbours should lead to complex effects of changes in grazing intensity on arrowgrass populations. This includes the potential for arrowgrass populations to increase for several years before declining, and for grazing intensity to have very little effect on arrowgrass populations over broad ranges over intensity. The model re-emphasizes the need for a better understanding of goose foraging: differences in arrowgrass population dynamics probably depend on the spatial distribution of geese.

In most field and laboratory experiments, including the ones described in this work, spatial and temporal scale are selected on the basis of feasibility and convenience. Recent work has suggested that this approach is likely to lead to misinterpretations when trying to extrapolate to scales other than the ones at which measurements were taken, and that more attention should be paid to temporal and spatial scales of interest *before* designing experiments (Addicott et al., 1987; Brown and Allen, 1989; Doak, 1991; Molofsky, 1994). Theoretical ideas and models have been developed to aid in the determination of appropriate spatial scales (e.g. Addicott et al, 1987; Senft et al., 1987; Urban et al., 1987) , but they have generally not been applied by field biologists. The experimental results elucidate processes occurring at different temporal scales which interact with each other, while the model results suggest that the temporal and spatial scales used will influence the conclusions drawn. Together they point towards three directions for future research on herbivore-plant relationships on the YK Delta: 1) detailed studies on goose foraging behaviour at the landscape level, the family (group) level, and the individual goose level, including changes in behavior with changes in vegetation structure; 2) longer-term population level studies of

arrowgrass, including spatial distributions at several scales; and 3) greenhouse and field studies on the role of competition between arrowgrass and other species. Gaining an understanding of this system will thus benefit greatly from integration of research interests and programs of plant and animal ecologists.

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